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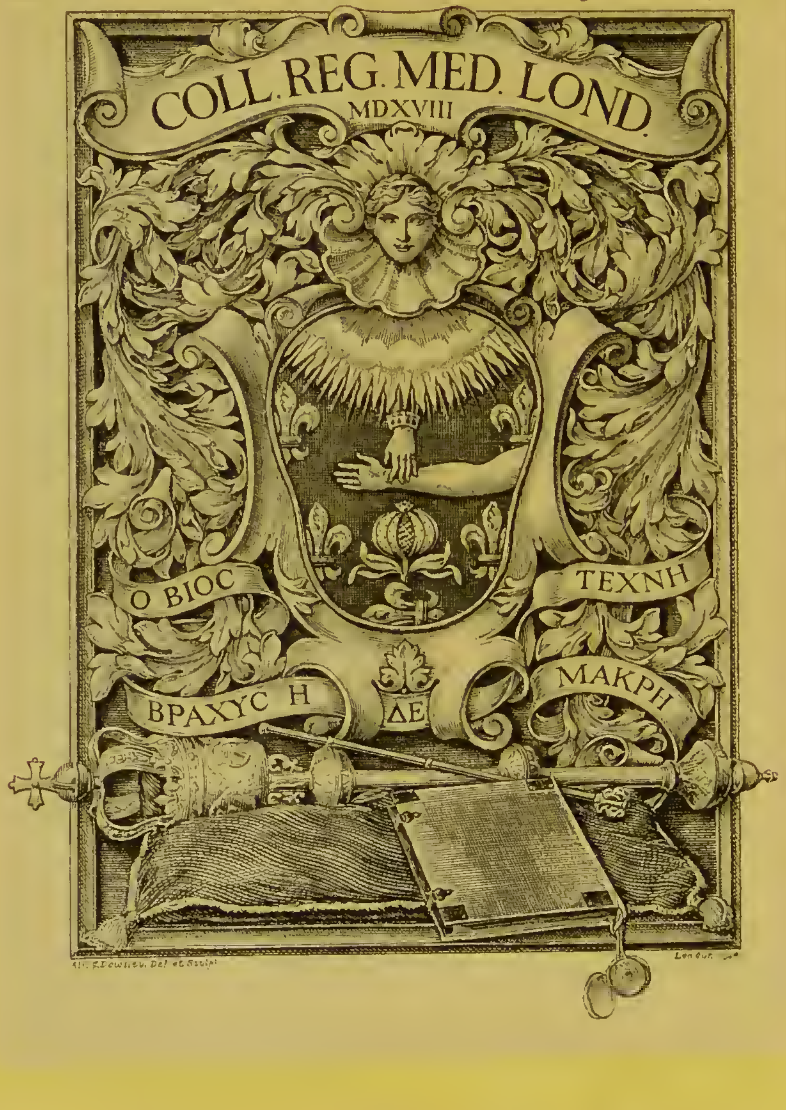

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REPORTS TO THE EVOLUTION COMMITTEE OF THE ROYAL SOCIETY.

REPORT I.—EXPERIMENTS UNDERTAKEN BY W. BATESON, F.R.S., AND MISS E. R. SAUNDERS.

(Presented to the Committee, Tuesday, December 17, 1901.)

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EXPERIMENTAL STUDIES IN THE PHYSIOLOGY OF HEREDITY.

By W. BATESON, M.A., F.R.S., and Miss E. R. SAUNDERS, Lecturer, Newnham College, Cambridge.

INTRODUCTION.

The experiments described in this Report were for the most part begun in 1897, and are still in progress. A part of the cost of the work has been defrayed from the Government Grant Fund, the sums thus received having been in part allotted to us by the Evolution Committee, and in part directly by the Grant Committee. The use of the garden in which the botanical experiments were carried out was kindly permitted during 1901, rent free, by the Botanic Garden Syndicate.

Following recognition of the fact that variations of animals and plants may be distinct phenomena, according as they are continuous or discontinuous, it seemed desirable to ascertain in as many cases as possible which variations belong to each of these categories. To answer this question specifically with regard to a diversity of forms, taking each character separately, and testing it by direct experiment in cross-breeding, was a primary object of our work. Such determinations must, in our judgment, constitute a first step in attempting to proceed with the problem of the nature and origin of Species.

Moreover, from what had been hitherto ascertained regarding the phenomena of heredity, the inference could scarcely be avoided that no universal law obtains, but that by studying various specific cases distinct specific laws may be detected.

Another object we have kept in view, is to test the possibility that in-breeding may have a specific effect in modifying the power of transmitting parental character to offspring. There are some indications,* derived from various sources, which point to such a possibility, and tend to show that an in-bred individual of a given breed A, when crossed with an individual of a different breed B, will be more likely to "transmit" the A characters to the offspring—in ordinary terms more "prepotent"—than another individual of the same breed A which was not in-bred, though equally pure or "thoroughbred." It did not appear that this possibility had been properly investigated by scientific methods, though otherwise expressed it is not unfamiliar to practical breeders. For example it is commonly believed that, *cæteris paribus*, a thoroughbred animal is more likely to stamp its own character on its offspring than an animal which is not a thoroughbred.

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* The most remarkable illustration of this phenomenon is that which is alleged

Thoroughbred animals are not rarely in-bred, and the possibility that the prepotency may be due to the in-breeding rather than the pure-breeding should be borne in mind. It is needless to emphasise the great practical and scientific consequences of such a proposition if it could be established.

Five years ago nothing could have seemed simpler, practical difficulties apart, than to investigate this question and to put it to an experimental test.* Meanwhile, however, as will presently appear, the whole problem of heredity has undergone a complete revolution, and the old idea of prepotency, if it is to be retained at all, must be otherwise conceived. Evidence of greater or less prepotency obtained by

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on the experience of breeders of so-called "light mules" between the canary and the goldfinch. Goldfinch mules are almost invariably bred between the canary hen and the cock goldfinch, for it is only exceptionally that the hen goldfinch breeds in captivity. It is stated that, in the vast majority of cases, the result of such mating is a "dark" mule, resembling the goldfinch in general colour. Very rarely the mule is light, *i.e.*, showing a good deal of the colour of the canary. At the cage-bird shows special classes and prizes are provided for such "light" mules, which are keenly sought for. It is stated by numerous writers on the subject that the probability of breeding "light" mules is greatly increased by using for the mother an in-bred—or, as is known in the fancy, a "sib-bred"—canary hen. This statement was, I understand, first publicly made by Mr. R. L. Wallace, the author of 'The Canary Book,' who there discusses the doctrine at length. However the truth may be, it is undoubtedly widely believed by mule-breeders, with the result that birds which are authenticated as "sib-bred" command an increased price. It is also asserted that since the promulgation of this theory light mules have become much commoner than they used to be. The possibility, however, should not be forgotten that the prepotency of the sib-bred hens *may* have been an original character of their particular strain, and we do not know any experimental *proof* that this prepotency has been brought about by consanguineous mating, though we think the latter hypothesis likely. [For further discussion, see p. 156.]

* Whether in-breeding between brother and sister as pursued in the poultry experiments has led to decline in fertility and weakness of constitution, is not really clear. We hope to publish details of experiences on this question when more material for comparison has been acquired. Such decline has been evident in some of the strains, but it is impossible to know how much of this is to be attributed to breeding from pullets before they are fully matured, or in some cases to late hatching.

methods formerly supposed satisfactory is now capable of different interpretations, and it is clear that to obtain a definite result on this point, a new set of precautions must be used. Consequently though some of the evidence to be adduced bears on the question of differential prepotency, we can offer as yet no plain answer to the original question, and some time must elapse before the matter can be definitely determined.

We expected, then, in chosen cases to determine the degree to which certain characters are discontinuous, whether they are capable of blending with their contraries or not, and to what degree their distinctness is maintained on crossing. In suitable cases we hoped further to determine specific laws of heredity, and to ascertain whether these laws can be affected by in-breeding the parental forms. It has always appeared to us that it can only be by *exhaustive study of special cases* that success can be attained in this direction, and that no results are as yet to be expected from partial experiment with a multitude of forms.

Upon these original objects and on several collateral subjects our experiments have given information. They are still, however, in the initial stage, and we hope to continue them in future years. We greatly regret that from want of space and appliances, we have been obliged to reduce the scope of our experiments to the barest limits. Investigations of this kind to be properly pursued—with animals at least—require far greater resources than we are able to command.

For many reasons we would rather have deferred publication until the work was further advanced, but we feel that with the re-discovery and confirmation of the principle which will henceforth be known as Mendel's Law, the study of heredity and the cognate problems of evolution must enter on a new phase.

At the present time the question how far Mendel's Law with its numerous corollaries is valid, to what cases and to what extent it is of general applicability, supersedes all others in significance. Consequently, our experience, however imperfect, since it bears directly on this question, has a value at this juncture, and we think it may be of use to the many investigators who will doubtless now turn their attention to the experimental study of heredity.

In the history of evolution it must ever be an astonishing fact that Mendel's discovery has so long remained unknown. The obscurity of the Brünn journal is a circumstance quite insufficient to explain the neglect of such a work.* No careful reader could doubt for a moment that he was in presence of true facts of exceptional significance. The reason may be that at the time of Mendel's publication, the announcement of the principle of Natural Selection had almost completely distracted the minds of naturalists from the *practical* study of evolution. The labours of the hybridists were believed to have led to confusion and inconsistency, and no one heeded them any more.

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* "Abh. naturf. Ver. Brünn," 1865, vol. 4, p. 1. The author of this remarkable paper, Gregor Johann Mendel, according to a communication made to Correns by Dr. von Schanz, was born in 1822 at Heinzendorf-bei-Odrau in Austrian Silesia. His parents were well-to-do peasants. In 1843 he entered the Königinkloster, an Augustinian house in Altbrünn and was ordained priest in 1847. From 1851–1853 he studied physics and natural sciences at Vienna. On retiring to his cloister he became a teacher in the Realschule of Brünn and afterwards Abbot. He died in

It is, perhaps, even more surprising that other investigators failed to discover the same law. Naudin's conclusions came very near it.

The literature of breeding teems with facts now palpably Mendelian. Gärtner, Godron, Laxton, even Darwin himself, must have been many times on the brink of the discovery.

Looking now at such experiments as those of Rimpau with wheat, &c., of Laxton with *Pisum*, Godron with *Datura*, of Darwin with Antirrhinum and sweet peas, we can hardly understand how the conclusion was missed. In Darwin's case no doubt the theory of Pangenesis contributed to difficulty, but some part of the obscurity must have been due to the habit of regarding various species, breeds, varieties, and casual fluctuations as all comparable expressions of one phenomenon, similar in kind; and to insufficient recognition of the possibility that variation may be, in its essence, specific. We may, perhaps, attribute to this preconception the extraordinary complexity with which his experiments on poultry and pigeons were arranged. Various breeds and various crosses were mixed together, and the results are not unlike those which the early chemists would have arrived at in testing the affinities and constitution of a number of unknown elementary and compound substances mixed together at random.

Mendel's Law.

In order to understand what follows it is absolutely necessary that the reader should have a general acquaintance with the present state of knowledge in regard to the Mendelian principle. The original paper is not easily accessible, but it has been reprinted in 'Flora,' 1901, and is about to appear in Ostwald's 'Klassiker der exakten Wissenschaften.' An English translation was published in the 'Journ. Roy. Hortic. Soc.,' 1901. We venture, however, to give a brief outline of the history and progress of the discovery, which is the more necessary

1884. His experiments were made in the garden of his cloister. Besides this paper he published a brief account of experiments with *Hieracium* in the same Journal, vol. 8, 1869, p. 26, and also various observations of a meteorological character. In 1853 and 1854 he published brief notes on *Scopolia margaritalis* and *Bruchus pisi* in the 'Verh. zool. bot. Ver. Wien,' but apparently no others dealing with natural history. Professor Correns informed us that he is said to have spent the later years of his life in the Ultramontane controversy. The Brünn Society, in 1865, was exchanging publications with most of the Academies of Europe, including the Royal and Linnean Societies.

as our own views and modes of expression do not agree wholly with those of other writers on the subject.

It may be premised that the first publication of the re-discovery was made in 1900 by de Vries,* and almost simultaneously by Correns† and Tschermak.‡ There can be no doubt that the appearance of this group of papers constitutes at length a definite advance both in the general study of the physiology of reproduction and in the particular problem of the nature of Species.

In 1865 Gregor Mendel published his discovery. His experiments are described in considerable detail, and the resulting law is stated with emphasis and precision. He at once perceived and lucidly enunciated what he regarded as the essential truth underlying the observed facts. A reader of this paper can hardly fail to recognise its masterly quality. By some strange chance it was ignored, and excepting a casual reference in Focke's 'Pflanzen-Mischlinge' (p. 110) there appears to be no allusion in literature to this remarkable performance. It is a fortunate circumstance that we need feel no hesitation in now accepting Mendel's account; for even if the original paper were such as to admit of doubt, the re-discovery comes to us with a large body of fresh evidence, the simultaneous work of three independent observers, confirming Mendel on the main points.

Mendel states that, like other investigators, he had been struck by the regularity with which offspring of certain hybrids reproduce the pure ancestral forms. But owing, as he supposes, to the complex nature of the cases studied and to want of accurate statistics, the precise facts had never been ascertained. Accordingly he set himself to work out some case from which every confusing element should as far as possible be excluded. After several trials he chose the varieties of *Pisum sativum* as best suited to his purpose. Besides other advantages, this species is well known to have the exceptional merit of being habitually self-fertilised, in N. Europe at least. From the many varieties of peas he first chose pairs of varieties, for crossing, in such a way that the members of each pair differed from each other in respect of one definite character. Of such pairs of characters he chose seven, namely: 1. Shape of seed, whether rounded *or* irregularly angular and deeply wrinkled. 2. Colour of cotyledons [" *endosperm*"], whether some shade of yellow *or* green. 3. Colour of seed-skin, whether a brownish shade *or* white (in correlation with white flowers). 4. Shape of ripe pod, whether simply inflated *or* deeply constricted between the seeds. 5. Colour of unripe pod, whether a shade of green *or* bright yellow. 6. Position of flowers, whether distributed along the stem *or* crowded near the top in a false umbel. 7. Length of stem, whether about 6—7 feet *or* about ¾—1½ feet. Between these various pairs of varieties crosses were then made, the female parent being emasculated.

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* De Vries, 'Comptes Rendus,' March 26, 1900, and 'Ber. deut. Bot. Ges.,' xviii, 1900, p. 83; *ibid.*, p. 435; 'Rev. gén. Bot.,' 1900, p. 257.

† Correns, 'Ber. deut. Bot. Ges.,' xviii, 1900, p. 158; 'Bot. Ztg.,' 1900, p. 232.

‡ Tschermak, 'Ztschr. f. d. landw. Versuchswesen in Oesterr.,' 1900, 3, p. 465.

As to the first two characters the result of the experiment is seen as soon as the cross-bred seeds are ripe; but to study the other five characters it is of course necessary to plant the seeds and grow the plants to maturity. On such examination it was found that in the case of each pair of characters one only was manifested in every cross-bred individual, to the total, or almost total, exclusion of the opposite character. The character which thus prevails is, in Mendel's terminology, the *dominant* (D), the character which is suppressed, being *recessive* (R). In the above enumeration of characters the dominant is placed first in each pair. Reciprocal crosses gave identical results. Briefly, then, D × R or R × D gave offspring which in appearance are all practically D.

The next generation is obtained by allowing the cross-bred plants DR to fertilise themselves. The result of such self-fertilisation is, according to Mendel, that the next generation instead of being uniform like their parents, breaks up into the two original forms. This takes place in such a way that there are on the average *three dominants to one recessive.*

The recessives are thenceforth not only apparently but *actually pure*, and if allowed to fertilise themselves give rise to recessives only, for any number of generations.

The dominants, on the contrary, though they may look alike, can, if allowed to fertilise themselves, be shown to consist of (*a*) individuals which are *pure* dominants, and on self-fertilisation give rise to dominants only; and (*b*) individuals which are cross-breds, and give rise on self-fertilisation to a mixture of dominants and recessives, *again in the proportion of three to one as before.* The *pure* dominants (*a*) are to the cross-bred dominants (*b*) as *one to two.*

The whole result, therefore, of self-fertilising the cross-breds is really 1DD : 2DR : 1RR, though apparently the proportion is 3D : 1R, because DR plants are not to the eye distinguishable from pure D.* The mixed offspring obtained by self-fertilising DR plants of this second generation consist again of D, DR, and R in the same proportions, and so on at each succeeding generation.

Mendel worked with considerable numbers, and it is impossible to doubt the general accuracy of his conclusions. In the case of some of the pairs of characters (notably the 5th) the evidence is much less clear than in the case of others, and it seems possible that in such cases unascertained disturbances may be at work; but on the whole the results, *as average results*, are clear. The purity of the pure dominants and pure recessives resulting from the self-fertilisation of the cross-breds was tested in the case of characters 1 and 2 to the sixth generation, for characters 3 and 7 to the fifth generation, and for characters 4, 5, and 6 to the fourth generation.

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* The attempt made by de Vries to indicate this result by an algebraical expression appears to us open to objection, and we prefer the simpler notation of Mendel.

Mendel interprets his facts as follows:—They point to the conclusion that in the cross-bred each of its pollen-grains and each of its egg-cells is *either pure dominant or pure recessive*,* *and that on the average there are equal numbers of each kind for each sex.* If the assortment of pollen-grains and egg-cells is then supposed to take place at random, the most probable percentage result is 25D ♀ × D ♂, 25D ♀ × R ♂, 25R ♀ × D ♂, and 25R ♀ × R ♂. As D × R does not differ from R × D, we have therefore 25D : 50DR : 25R. But as cross-breds resemble dominants in appearance, the *apparent* result is 3D : 1R at each successive self-fertilisation of cross-breds.

Mendel next proceeded to cross pairs of varieties differing in respect of *two* characters; for example, a variety having seeds round and yellow with a variety having seeds angular and green; and also pairs of varieties differing in *three* characters; for example, a variety characterised by seeds round, yellow, and in grey-brown skins with a variety having seeds angular, green, and in white skins. The numerical results of these experiments are set out at length, and are too long to repeat. Briefly the result in all cases was that the dominant characters alone appeared in the first cross. When these were self-fertilised, in the case of *two* differentiating characters, *four* different kinds of seeds resulted, namely, round yellow, angular yellow, round green, and angular green. In the case of *three* differentiating characters these were similarly combined in the *eight* possible combinations. In both sets of experiments the numbers of individuals and their constitution, as tested by the seeds they were capable of producing on self-fertilisation, were consistent with the hypothesis arrived at in the case of varieties differing in respect of one character, namely, that each male and female cell of the cross-bred is pure in respect of one character of each pair of characters, and is capable of transmitting this character to the exclusion of the opposite character; that the reproductive cells are, in the cross-breds, of as many kinds as there are possible combinations of pure characters (taken two or three together, as the case may be); and, finally, that each kind is represented in the cross-breds on the average in equal numbers.

Mendel next tested the truth of the hypothesis that both male and female cells were similarly differentiated, by crossing the first crosses with pure D and pure R forms respectively, finding, as he expected, that DR × D gives the ratio 1DD : 1DR, and that DR × R gives on the average the ratio 1DR : 1RR. Both sets of germ-cells are therefore similarly differentiated.*

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* In what follows such forms are spoken of as "extracted" dominants, or "extracted" recessives.

It must be understood that this condensed statement does no justice to the lucidity and completeness of Mendel's account of his facts, and of the reasoning based on them. With regard to the numbers, it may be said that though there is a good deal of irregularity, yet taken together they plainly bear out the law as a statement of average results.

De Vries† working with pairs of varieties belonging to a diversity of genera and species, found that in a large number of cases one of the varietal characters was definitely dominant, prevailing in the first crosses to the exclusion of the recessive character. In several of these cases the offspring of the cross-breds fertilised *inter se* were mixed dominants and recessives in proportions fairly agreeing with Mendel's law. In the case of two colour varieties of *Papaver somniferum*, the constitution of the resulting dominants was investigated, and shown to be also according to the law. In certain cases also the purity of the recessives was tested and found to be complete.

De Vries' first announcement was followed almost immediately by the appearance of a paper by Correns,‡ giving an account of some years' work with peas, repeating Mendel's experiments and confirming them as regards the colour of the seeds.

Correns stated that he has tested the purity of the pure dominants and pure recessives to the third generation, and he has kindly informed us that a fourth generation is equally pure.

In addition to these, Tschermak has given an account§ of simultaneous investigations also carried out on varieties of peas. This last paper is an elaborate memoir giving in addition valuable information on several points not directly relating to the present subject.

Tschermak worked with many varieties of peas, and though he obtained several results not wholly consistent with Mendel's law, and some actually conflicting evidence, the general tenour of his work is confirmatory. He gives, in particular, results as to the crossing of cross-breds with one or other of the pure forms.

It is an obvious corollary from Mendel's law that the cross-bred crossed with the recessive parent should give seeds of the dominant and recessive colours in equal numbers. On the other hand, the cross-bred crossed with the dominant should give dominants only (of which half should be pure and half cross-bred in composition). Tschermak's numbers though insufficient for a thorough test, are in fair harmony with Mendel's hypothesis. He believes also that there is evidence that yellow is more decidedly dominant over green than the rounded character is over the wrinkled, and on this point further experiments are required.

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* As it happens, almost all our breedings of cross-breds with pure types have been in the form cross-bred ♀ × pure ♂, but reciprocal experiments are in progress.

† C.R., 1900, March 26; 'Ber. deut. Bot. Ges.,' 18, 1900, p. 83.

‡ 'Ber. deut. Bot. Ges.,' 18, 1900, p. 158.

§ 'Ztsch. f. d. landw. Versuchswesen in Oesterr.,' 3, 1900, p. 465; continued later, *ibid.*, 4, 1901, p. 641, and 'Ber. deut. Bot. Ges.,' 19, 1901, p. 35.

Subsequently a paper by Correns* has appeared describing his experiments with a glabrous and a hoary form of garden stock (*Matthiola incana*), and giving results as to these varieties, tested by self-fertilisation, and also by recrossing the cross-breds with the parental forms. In this, as in each of the other papers, there are many points which call for separate notice and discussion, but the facts taken together are in fairly close agreement with the expectation given by Mendel's law, though the discrepancies are decidedly greater in this case than in the others. The case happens to be one which had also formed a subject of our experiments, and the various questions raised by the facts will be discussed in connection with the statement of our results.

Lastly, Professor Correns has also published† an elaborate and important memoir on the results obtained in crossing varieties of maize. Some of these results are of a complex character, but the essential fact of the truth of Mendel's law in its application to many of these cases was fully established. From the striking differences between these varieties in several characters, notably in the constitution of the endosperm, whether round starchy (dominant) or wrinkled and sugar-containing (recessive), this case is a most attractive subject for such experiments.

In the characters of the endosperm in maize de Vries‡ also demonstrated the truth of Mendel's law. As regards the colour varieties, Correns showed many complications to exist owing to the fact that the general appearance of the seed depends partly on maternal and partly on embryonic elements; and in some of the characteristics there are other confusing factors owing to fluctuations in the intensity of the dominance.

The above is a brief sketch of a vast mass of observations all tending to the same conclusion, and the truth of the law enunciated by Mendel is now established for a large number of cases of most dissimilar characters, beyond question.

Let us now shortly distinguish what is essential in the new discovery from what is not. The fact that in the cross-bred one character, in appearance, dominated to the exclusion of the other is not of the essence of Mendel's discovery. Tschermak, for instance, saw some exceptions to this rule in *Pisum*. Among the *Matthiola* crosses here described, and among those originally made by Trevor Clarke,* the hoary form *seems* to be not exclusively dominant. Correns saw considerable fluctuations in the dominance of the colours of maize. It is practically certain some of the poultry cases about to be described exhibit the same phenomenon. In fact, generally speaking, there are good reasons for thinking that in numerous instances purity of gametes may occur without either character exhibiting dominance.

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* 'Bot. Cblt.,' 1900, 43, p. 97.

† 'Biblioth. Bot.,' 1901, Heft 53.

‡ 'Rev. gén. Bot.,' 12, 1900, p. 270.

There is also some reason for supposing that alterations in dominance may be affected by changes in conditions (see p. 136), and possibly even by differences in the state of the parents, though the only considerable body of evidence relating to these points, obtained by Vernon† in Echinid crossing, still needs repetition and confirmation.

The essential part of the discovery is the evidence that *the germ-cells or gametes produced by cross-bred organisms may in respect of given characters be of the pure parental types and consequently incapable of transmitting the opposite character*: that when such pure similar gametes of opposite sexes are united together in fertilisation, the individuals so formed and their posterity are free from all taint of the cross; *that there may be, in short, perfect or almost perfect discontinuity between these germs in respect of one of each pair of opposite characters.*

Doubt might naturally be felt as to the acceptance of a proposition so far-reaching, but it is impossible to see any other possible interpretation of the facts. The pure dominant and pure recessive members of each generation are not merely like, but identical with the pure parents,‡ and their descendants obtained by self-fertilisation are similarly pure. If they are pure, surely the male and female elements of which they were composed must also be pure.

In another part of this Report we propose to discuss the bearing of these remarkable facts, and to show some of the conclusions to which they point. It will be seen that they provide satisfactory interpretations of some of those redoubtable paradoxes which have hitherto been so mysterious to all evolutionists.

We may now proceed to the description of our own experiments.

LEPIDOPTERA.

In addition to the work here described experiments were made in crossing *Pieris napi* with the var. *bryoniæ*, and *Pararge egeria* with the var. *egerides*. These crosses were pursued for some years until the strains were exterminated by disease.

The results are not altogether consistent, and in the case of *Pieris*

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* 'Rep. Intern. Hort. Exhib. and Bot. Congr.,' 1866, p. 142. As the sequel will show, this appearance is otherwise explicable

† Vernon, H. M., 'Phil. Trans.,' B, 1898, vol. 164, p. 465.

‡ Correns, in maize, has found an apparent change in the degree of dominance of certain characters in the "extracted" variety.

napi are highly complex. In the light of present knowledge we desire to repeat these experiments, and we hope to clear up some of the difficulties before publishing. To those who have leisure for such work, we suggest these species as offering unusually good opportunities for investigating problems of heredity, and we should be glad to communicate with any one who cares to undertake such work.

PART I.—EXPERIMENTS WITH PLANTS, CARRIED OUT BY E. R. SAUNDERS.

Choice of Subjects for Experiment.

In "The Variation of Animals and Plants under Domestication,"* Darwin mentions among other instances of plants in which the absence of blending of the parental characters in the offspring is well-marked, the case of certain hoary and glabrous varieties of garden stocks; when these varieties were intercrossed the foliage of the offspring resembled one or other of the two parents, and intermediates did not occur. The evidence upon which this statement rests is furnished by the experiments of Trevor Clarke, a brief reference to which is found in the 'Gardener's Chronicle,'† and a fuller statement in the Report of the Proceedings of the International Horticultural Exhibition and Botanical Congress, held in London in 1866.‡

In these experiments the "little annual glabrous-leaved stock of the nurserymen" was crossed with pollen from a large hoary biennial form (*Cocardeau* of the French); the result was that one half of the seedlings were glabrous or "Wall-flower leaved," and the other half rough like the male parent—none were intermediate in leaf character.

The glabrous seedlings were, however, no longer dwarf but "of tall and strong habit." The author further states that succeeding generations raised from the hoary cross-breds produced a percentage of glabrous plants, but that the converse was not observed and probably did not occur. Moreover these experiments were verified by repeated trials, which were followed in every case with the same result. Similar results were obtained from intercrossing races which differed in seed colour, as *e.g.*, a purple flowered Queen stock with black seeds, and a red flowered stock with brown seeds. These statements suggested that the stock would afford excellent material for statistical experiments upon cross-breeding. The choice of this genus has, moreover, the following advantages: the plants are hardy and flower freely; the flowers are fairly easy to handle; self-fertilisation occurs in the course of nature, so that a succession of generations, thus raised, can be obtained without other treatment than that of covering the flowers; the seeds germinate readily and they are easily harvested, since the fruits can be gathered before they dehisce.

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* Ed. 2, vol. 2, p. 71.

† 1866, p. 588.

‡ p. 143.

As a like case of complete discontinuity in the character of the leaf surface had also been observed by de Vries in the case of *Lychnis vespertina* and its glabrous variety, a parallel set of experiments was therefore carried out with the hoary forms *vespertina* and *diurna*, and white and red flowered glabrous varieties. All the forms are diœcious, and thus possess a two-fold advantage, there is no question of emasculation, and consequently no possibility of accidental self-fertilisation through faulty manipulation.

In addition to the above, two other genera were selected for experiment, viz., *Atropa Belladonna* type form and var. *lutea*, both of which at the time were available in the Cambridge Botanic Garden, and *Datura Stramonium* and *D. Tatula*, of which the prickly and smooth fruited forms have appeared to more than one of the earlier workers on hybridisation to be favourable subjects for investigation.*

These experiments were begun in 1897; in 1900 de Vries published the papers† in which he draws attention to the results obtained by Mendel, and enumerates various cases in which he finds that Mendel's law holds, including among them *Lychnis vespertina* type form and var. *glabra*, and *Datura Tatula* and *Stramonium*. Later in the same year Correns‡ published an account of his experiments upon *Matthiola*, showing to what extent Mendel's law applies in the particular races of stocks which he employed. In addition to the work of these observers it seems desirable at this point to give a full statement of the statistical results obtained in our experiments, especially as in the case of Matthiola they have revealed more complex issues than appear in the simple case examined by Correns.

Throughout these experiments the flowers to be fertilised were emasculated (when hermaphrodite), and covered before the dehiscence of the anthers and the unfolding of the corolla, while the pollen was usually taken from covered flowers, or from buds picked while still unopened; in the case of some hoary strains of stocks growing alone or at a distance from those under experiment, this latter precaution was considered unnecessary. In both Atropa and Datura the habit of the plant and the disposition of the flowers render it easy to place the buds expanding simultaneously on any individual under separate covers, an arrangement which minimises the possibilities of error; to have attempted to secure similar conditions in Matthiola, in which the flowers are closely crowded and open in rapid succession, would have involved an expenditure of labour, or a sacrifice of material which would not have been possible without seriously reducing the number of experiments: except in special cases therefore, it was not attempted.

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* Koelreuter, Gaertner, Naudin, Godron. For the literature see Focke, 'Die Pflanzen-Mischlinge,' 1881, p. 263.

† 'Comptes Rendus,' March 26, 1900, and 'Ber. Deut. Bot. Gesell.,' Bd. 18, 1900, p. 83.

‡ 'Bot. Centralblatt,' Bd. 84, 1900.

Preliminary Statement of Results.—It may be stated at once that the phenomena in Lychnis, Atropa, and Datura follow Mendel's law with considerable accuracy, and no exceptions that do not appear to be merely fortuitous were discovered.

In the case of Matthiola, the phenomena are much more complex. There are simple cases which follow Mendelian principles, but others of various kinds which apparently do not. The latter cases fall into fairly definite groups but their nature is still obscure.

In the following pages it will be convenient to deal with the simpler cases first.

LYCHNIS.

The two forms *L. vespertina* and *L. diurna* were each intercrossed with white-flowered and red-flowered glabrous varieties. *L. vespertina* is a native of Cambridgeshire, and wild plants were therefore easily procured in the neighbourhood; *L. diurna* is not found in the county, and seeds of this form were collected in Cornwall. For the glabrous varieties, which were at the time growing in the Cambridge Botanic Garden, we are specially indebted to Professor de Vries.* All the forms are perennial.

The discontinuity between the hairy and the glabrous forms appears to be absolute; among the whole number of plants raised, not a single intermediate was observed. Such, however, is not the case when characters other than leaf surface are considered, as *e.g.*, colour of corolla (white or red), position of capsule teeth (erect or recurved), colour of seed (grey or black). When a cross was made between the types differing in respect of these latter characters, the offspring exhibited a series of intermediate forms. The corolla varied from the deep red of *diurna* to the palest pink, but was rarely, if ever, pure white; the capsule teeth might be directed obliquely upwards, as in *vespertina*, or be turned downwards and slightly recurved, or be in any intermediate position; but the rolled form characteristic of *diurna* was extremely rare. The seeds were of all tints from yellowish-grey to black.†

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* The discovery by de Vries of a wild specimen of *L. vespertina*, var. *glabra*, and the artificial production from it of a smooth red-flowered form are described in his 'Erfelijke Monstrositeiten," p. 10 (p. 26 of the French translation); he names this red-flowered form *L. diurna*, var. *glabra*. It may be noted, however, that such plants grown at Cambridge from his seed, although resembling *diurna* in the colour of the corolla, had not the recurved teeth characteristic of the capsule in that form; on the contrary, they were in this respect similar to the white-flowered form (*L. vespertina*, var. *glabra*) from which they were originally descended. The characters of hairiness and of the capsule-teeth are therefore dissociable.

† For a detailed description of hybrids of *L. diurna* and *L. vespertina* see Gagnepain, 'Bull. de la Soc. Bot. de France,' 1897, Tomes 43 and 44.

The results as regards hairiness are tabulated in the succeeding pages, in which the different forms are briefly indicated as follows:—

WH = *L. vespertina*, plant hairy, flowers white.
RH = *L. diurna*, plant hairy, flowers red.
WG = Glabrous variety with white flowers.
RG = ,, ,, ,, red ,,

In all cases the cotyledons are glabrous, but the seedlings can be sorted as soon as the next pair of leaves appear. In the glabrous varieties no hairs were observed upon any part of the plants at any time.

Table I.—First Cross-bred Generation obtained by crossing the Hairy and Glabrous Forms in each of the eight possible ways.

Parentage.*	Number of seed parents.	Number of flowers.	Number of offspring.	
			Hairy.	Glabrous.
WG × WH........	5	6	91	
WG × RH	2	3	63	
RG × RH	4	6	133	
RG × WH........	1	4	126	
WH × WG........	4	12	100	
WH × RG	1	1	3	
RH × RG	3	11	208	
RH × WG........	2	9	282	
Total...........	Individuals used more than once.	52	1006	0

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* Throughout the paper expressions in the form A × B indicate that A is the seed parent and B the pollen parent.

Table II.—Offspring of Cross-breds when fertilised *inter se.**

Parentage.	Number of seed parents.	Number of flowers.	Number of offspring.		Totals for each particular kind of union.	
			Hairy.	Glabrous.	Hairy.	Glabrous.
(RH × RG) × (RH × RG)	1 1	2 1	17 82	6 21	99	27
(RH × WG) × (RH × WG)	1 1	1 1	31 11	12 4	42	16
(RG × RH) × (RG × RH)	1 1 1	2 1 2	47 62 28	17 14 10	137	41
(RG × WH) × (RG × WH)	1	1	59	14	59	14
(WG × WH) × (WG × WH)	1 1	1 2	15 37 7	6 16 2	59	24
(WG × RH) × (WG × RH)	1	1	12	4	12	4
Total	..	..	..	..	408	126

Expected result, 3 : 1; actual result, 3·2 : 1

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[*] As all the forms employed are diœcious, fertilisation of the cross-breds *inter se* is necessary where the alternative of self-fertilisation would be possible with hermaphrodite types.

Table III.—Offspring of Cross-breds when crossed with the original Recessive (Glabrous) Form.

Parentage.	Number of seed parents.	Number of flowers.	Number of offspring.		Totals for each particular kind of union.	
			Hairy.	Glabrous.	Hairy.	Glabrous.
(WH × WG) × WG	1	1	31	27	220	211
	1	1	67	60		
	1	2	77	75		
	1	2	45	49		
(WG × WH) × WG	1	2	18	25	18	25
(RH × RG) × RG	1	1	4	4	110	95
	1	2	16	11		
	1	3	90	80		
(RH × WG) × WG	1	1	9	7	39	42
	1	3	7	5		
	1	2	14	24		
			9	6		
(RG × RH) × RG	1	2	13	16	60	60
	1	3	47	44		
Total	..	..	..	..	447	433

Expected result, 1 : 1 ; actual result, 1·0 : 1.

Table IV.—Offspring of Cross-breds when crossed with the original Dominant (Hairy) Form.

Parentage.	Number of seed parents.	Number of flowers.	Number of offspring.	
			Hairy.	Glabrous.
(RG × RH) × RH	1	1	35	
(RH × RG) × RH	1	1	6	
Total	2	2	41	0

Table V.—Offspring obtained by fertilising the Offspring of the Cross-breds *inter se*, (α) when both the final parents are hairy.
(β) ,, ,, ,, ,, glabrous.

Parentage.	Number of seed parents.	Number of flowers.	Number of offspring.	
			Hairy.	Glabrous.
(*a.*)				
[(WG × WH) × WG] × [(WG × WH) × WG]	1	1	23	6
[(RG × RH) × RG] × [(RG × RH) × RG]	1	1	87	25
Total	2	2	110	31
Ratio			3·5 : 1	
(β.)				
[(WG × WH) × WG] × [(WG × WH) × WG]	1	2		43
[(RG × RH) × RG] × [(RG × RH) × RG]	1	1		8
Total	2	2	0	51

A glance at the preceding tables will show—

(1) That the hairy character is dominant and the glabrous recessive (Table I). Of the thousand cross-breds raised from various unions between hairy and glabrous strains, all, without exception, were hairy.

(2) That such cross-breds invariably yielded both dominant and recessive forms if fertilised *inter se* (Table II), or if crossed with the recessive form (Table III); in the former case in the proportion of (about) 3 D to 1 R, in the latter of 1 D to 1 R; but that when crossed with the dominant form the offspring are again all dominant (Table IV).

(3) That when the offspring of cross-breds were intercrossed, like with like, the result varied according as they were of dominant or recessive form. Recessives fertilised *inter se* yielded only recessives (Table V*b*), but dominants (two individuals) similarly fertilised, yielded dominants and recessives in the ratio 3·5 : 1, thus proving impure dominants (dominant hybrids) which yield both forms in the succeeding generation; had either parent in either case been a pure dominant, the offspring would presumably have been all dominant (see Table IV).

These results clearly show that in the above-mentioned forms of Lychnis we have excellent illustration of a case to which Mendel's law is wholly applicable as regards the particular character of leaf surface.

ATROPA.

I. *First Cross-bred Generation.*

Reciprocal crosses were made between two individuals of *A. Belladonna typica* (flowers brown, fruits black, stem tinged with red = B), and a vigorous specimen of *A. Belladonna*, var. *lutea* (flowers and fruits yellow, stem pure green = Y).* Both forms are perennial.

From crosses of the form B × Y 100 plants were raised, and from the reciprocal unions Y × B, 236. In both sets of cross-breds the fruits (numbering in the three years, during which the plants have been under observation, some thousands) were all black, and though the flowers showed several shades of brown they never varied to pure yellow. The stems were more or less deeply tinged. It would appear then that the colour of the type form is completely dominant in the fruit of the cross-bred, but that in the corolla and stem the intensity of the dark coloration may be more or less diminished.†

II. *Offspring of Cross-breds.*

Twenty-five flowers on as many cross-breds were self-fertilised, but (in consequence perhaps of self-sterility) set no fruit; offspring were therefore obtained by fertilising the cross-breds with pollen from the parent forms.

(α) *Cross-bred* × *Dominant.*—Flowers on 21 individuals (20 Y × B and 1 B × Y) were crossed with the dominant form; 220 (197 and 23) plants were raised, and all bore black fruits. As in the first cross-bred generation there was complete dominance of the type colour.

β. *Cross-bred* × *Recessive.*—Flowers on 38 individuals (22 Y × B and 16 B × Y) were crossed with the recessive form, and the seeds of each plant sown separately. In every case a mixed lot of seedlings was obtained, differing in the colour (green or reddish) of the young stem (hypocotyl). Unfortunately a late frost killed an enormous number of the seedlings, before any attempt had been made to estimate at all accurately the total numbers of the two colours; it had, however, been noted, that up to this time there appeared to be either rough equality or a slight preponderance of the pure green. Of those that survived many perished before flowering, owing to the dryness of the season, so that eventually less than 300 plants lived to bear fruit; of these, all those with green stems bore yellow flowers and fruits, those with reddish stems brown flowers and black fruits, but the latter were more than twice as numerous as the former (197 B, 75 Y). In view of the earlier observation on the seedlings, however, it seems extremely doubtful whether any reliance can be placed upon the final numbers. Although, therefore, all that can be stated with certainty is that there is complete agreement with Mendel's law in so far—(1) that the fruit colour of the type form is completely dominant in the first cross-bred generation, whether the cross be of the form D × R or R × D; and (2) that the offspring resulting from a union between a cross-bred and a pure dominant are all dominant, but that when the cross is made with a pure recessive the offspring are mixed dominant and recessive; nevertheless, the observations made at the time of germination suggest that this agreement would probably prove quantitative as well as qualitative.

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* There was no difficulty in manipulating this cross, nevertheless few flowers set fruit; 250 were crossed and only about a dozen set seed. The fruits that were formed had a full complement of seed.

† Hoffmann obtained a similar result with these two forms; he states that cross-breds, whether offspring of typica × lutea or lutea × typica, in the two seasons during which they were observed bore only black fruits. The experiments were not apparently continued beyond the first generation. 'Ber. Oberhessische Gesell. für Natur. u. Heilkunde,' 16, s. 14.

DATURA.

The following forms were employed—

1. *D. Stramonium* (stems green, flowers white, fruits prickly).
2. *D. Stramonium*, var. *inermis* (stems green, flowers white, fruits smooth).
3. *D. Tatula* (stems reddish, flowers violet, fruits prickly).
4. *D. Tatula*, var. *inermis* (stems reddish, flowers violet, fruits smooth).

Reciprocal crosses between these different types showed clearly that of the two pairs of antagonistic characters the violet colour is dominant, the white recessive, and similarly that the armed condition is dominant and the unarmed recessive; also that these results obtain whichever combination of forms is employed.

Several earlier observers have selected the various species of Datura as affording suitable material for the study of hybrids. Naudin* crossed *D. Stramonium* with *D. Tatula*, and *D. Tatula* with *D. Stramonium*, and found that in both cases the first generation of cross-breds resembled *D. Tatula*; in the second generation both the parent forms appeared, but *D. Tatula* was more abundant than *D. Stramonium*—the actual figures are not given. Similarly with *D. Stramonium* and *D. lævis*, the first generation resembled *D. Stramonium*, the second produced both forms. Later Godron's† results appeared with a record of the numbers obtained. This observer found that *D. Bertolonii*‡ crossed with *D. Tatula* yielded offspring all resembling *D. Tatula*; but that among the 29 plants obtained in the second generation three distinct forms occurred, viz., *Tatula*, *Tatula* var. *inermis*, and *Stramonium*, and in the proportion respectively of 16, 11, and 2. It will be noticed that with both observers *Tatula* was found to be a dominant form. As regards Godron's second result, a comparison with the following tables would seem to show that the numbers in the second generation are too small to afford conclusive evidence either as to the possible number of forms which may result from this particular union, or as to the relative abundance of each.

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* 'Nouv. Arch. Mus.,' 1, p. 41; for the earlier literature, see Focke's 'Pflanzen-Mischlinge,' p. 263.

† 'Mém. Acad. Stanisl.,' 1864, 1865, 1872.

‡ *D. Bertolonii* of Godron = *D. Stramonium*, var. *inermis*. *D. lævis* of Naudin is a white-flowered unarmed form not very different from this.

From two other experiments described by Godron it would appear that the offspring of cross-breds *may* exhibit a character which had not (presumably) been introduced by either of the original parents; *e.g.*, *Stramonium* × *Tatula* yielded in the second generation the four forms *Stramonium*, *Bertolonii*, *Tatula*, and *Tatula*, var. *inermis*, although neither of the original parents possessed unarmed fruits. Again from a cross between *Tatula* and *Tatula* var. *inermis*, he obtained in the second generation both the parent forms, and also *Bertolonii*, although both parents were of the dominant colour.

In each case it will be noticed that the unexpected form of offspring belonged to a recessive type. These results are at variance with those detailed below, but in the light of the facts which we now know, a possible explanation of these apparent contradictions at once suggests itself. May it not be that one (or both) of the crossed forms, although apparently pure, was in reality a cross-bred—an impure dominant—exactly resembling the pure dominant type which it was intended to employ? Godron states that the type forms were grown together in the same garden, and that he had been led to conclude that it was not necessary to cover the flowers in order to avoid chance cross-fertilisation. If then it is also borne in mind that a plant which in fruit-form, and in the colour of stem and flower has all the appearance of a specimen of *D. Tatula*, may, nevertheless, when self-fertilised, prove by its mixed offspring that it is not "pure" but a cross-bred derived from a cross with any one of the three forms *Tatula* var. *inermis*, *Stramonium*, or *Stramonium* var. *inermis*; it seems not impossible that such an unsuspected cross-fertilisation may have occurred among Godron's plants; for the effect of such a cross is not immediately apparent—not, in any case, until the next generation but one. These considerations suggest a very necessary precaution in all experiments of this kind, viz., the carrying out of control experiments in order to test the purity of the parent plants. When the immediate parentage of the individuals selected for crossing is unknown, the self-fertilisation of additional flowers would yield valuable evidence in corroboration (or otherwise) of the results obtained by cross-fertilisation. The importance of such controls in cases of complete dominance is obvious. The alternative hypothesis is, of course, that an original variation occurred.

Although the offspring resulting from a cross between any two of the forms employed are usually indistinguishable from the type which is dominant as regards the particular character crossed, yet in other cases the intensity of a dominant character may be more or less diminished either in particular individuals or in particular parts of one individual. In Tatula-Stramonium cross-breds the corolla is often paler in colour than that of the dominant parent (as has already been noticed by Naudin),* but even in the palest specimens the deep blue colour of the unopened anthers leaves no doubt as to the presence of the dominant colour element. When the seedling offspring of these cross-breds are sorted into groups according to the pure green or reddish-green colour of the hypocotyl, it was noticed that the tint in the red-stemmed individuals was not equally pronounced in all cases. The occurrence of intermediate forms was also occasionally noticeable in the fruits. Among the large number of capsules examined, there were some of the mosaic type, in which part of the capsule was prickly and the remainder smooth, while others, suggesting a blend, were more or less prickly all over, but the prickles were much reduced in size, and often formed mere tubercles. These mosaics occurred as rarities both on prickly individuals and on smooth ones still more rarely. Naudin observed the not uncommon occurrence of both these intermediate forms, but Godron† only records a single instance. Such intermediate fruits were most often found towards the end of the flowering season; occasionally, however, the first fruit of all was smaller than the others, and in that case often less prickly also. Increase in height and sterility of the flowers at the lower bifurcations occurred among the cross-breds, but to the slight extent observed by Godron, rather than in the more pronounced degree described by Naudin.

In one cross Godron obtained from *Stramonium* × *Bertolonii* plants all like *Bertolonii*, as stated. Among their offspring three forms appeared, *Stramonium*, *Bertolonii*, and *Tatula inermis.* These results are at variance with ours obtained from the reciprocal cross (*Stramonium inermis* × *armata*). Here the offspring resembled *armata*, and in the next generation only the parent-types *armata* and *inermis* came. Moreover, in no other experiment with these types has a dominant character (whether armed fruits or coloured flowers) appeared among the offspring of recessives. Yet in this one case both results are said to have occurred. Here the use of a DR by mistake for DD would not explain the contradiction, and we must suppose either that this is a true exception, or that error occurred in the experiment or description.

An analysis of the results of the various unions is shown in the following tables, in which the parent forms are indicated by the abbreviations T. ar., T. in., S. ar., S. in.

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* *Loc. cit.*

† *Loc. cit.*

I. *First Cross-bred Generation.*

Table VI.

Parentage.	Number of seed parents.	Number of flowers.	Number of offspring.			
			T. ar.	T. in.	S. ar.	S. in.
T. ar. × T. in. . .	2	3	28 23 17			
		Total	68	0	0	0
T. in. × T. ar. . .	1	1	28			
		Total	28	0	0	0
S. ar. × T. in. . .	1	1	61			
		Total	61	0	0	0
T. in. × S. ar. . .	1	1	41	1		
		Total	41	1	0	0
S. in × T. ar. . .	3	3	43 20 20			
		Total	83	0	0	0
S. in. × S. ar. . .	7	8		61 53 36 32 18 18 18 2		
		Total	0	238	0	0

The cross T. ar. × S. in. was also made, but for some reason the seeds failed to germinate. From seeds of this cross (kindly sent by Professor de Vries), however, twenty plants were obtained, all resembling the type T. ar.

It will thus be seen that more than 500 cross-breds were obtained from seven different unions between the four type forms, and that, if we except a single plant,* the uniform result is that when armed and unarmed races are intercrossed the armed character is dominant, and that when Tatula and Stramonium forms are crossed together the dark colour of the former is also dominant.

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* This plant bore a single undersized smooth fruit; as no flowers were subsequently produced, further evidence as to the true character of the plant could not be obtained. But in view of the uniformity of the results as regards the complete dominance of the armed character in all other cases, it seems at least possible that a stray pollen-grain or a stray seed may account for this solitary exception.

II. *Offspring of Cross-breds.*

(α.) When Tatula *or* Stramonium cross-breds are self-fertilised.

Table VII.

Parentage.	Number of seed parents.	Number of flowers.	Number of offspring.					
			Number of seedlings.		Number of plants which matured fruits.			
			T.	S.	T. ar.	T. in.	S. ar.	S. in.
(T. ar. × T. in.) × self	3	3	62 31 30		19 18 24	1 6 5		
		Total	123	0	61	12	0	0
(T. in. × T. ar.) × self	2	2	49 34		19 all killed by frost.	6		
		Total	83	0	19	6	0	0
(S. in. × S. ar.) × self	4	4		54 49 10 8			27 34 6 5	16 5 2 2
		Total	0	121	0	0	72	25

Table VII shows that when cross-breds derived from unions between armed and unarmed races of *like* colour were self-fertilised, the offspring also were of one colour, uniform with that of the parents; but that as regards the fruits, they were in each case divisible into two groups, having respectively the types of capsule characteristic of the two parents. In two sets out of the three the totals approximate very closely to the expected ratio 3D : 1R, though individuals gave wide results; the remaining set, it will be noticed, includes one case in which there is a considerable discrepancy between the theoretical 3 : 1) and the observed (19D, 1R) result. The explanation possibly ies in the fact that more than two-thirds of the seedlings perished, and therefore the final numbers may not represent at all accurately the original proportion of the two forms. If this case be excluded, the agreement is fairly precise.

(β.) When Tatula–Stramonium cross-breds are self-fertilised or fertilised *inter se*.

Table VIII.

Parentage.	Number of seed parents.	Number of flowers.	Number of offspring.					
			Number of seedlings.		Number of plants which matured fruits.			
			T.	S.	T. ar.	T. in.	S. ar.	S. in.
(T. ar. × S. in.) × self or *inter se*	6	6	37	20	17	5	5	2
			18	7	11	4	2	—
			25	9	21	2	6	—
			45	17	33	9	14	—
			28	8	20	6	6	1
			17	12	15	2	9	2
		Total	170	73	117	28	42	5
(S. in. × T. ar.) × self	2	2	266	92	18	16	4	3
			Not recorded.		22	9	14	2
		Total	?	?	40	25	18	5
(T. in. × S. ar.) × self	6	7	58	28	2	1	—	—
			29	11	7	1	2	2
			80	29	14	5	8	1
			60	23	5	1	5	—
			64	19	15	3	4	—
			7	3	4	1	2	—
		Total	298	113	47	12	21	3

In Table VIII we have the corresponding results obtained from cross-breds when the original parents *differed not only in the character of the fruit, but also in colour.* In the first two cases the two dominant and the two recessive characters were distributed in different parents; in the third each parent combined one dominant with one recessive character. On the Mendelian hypothesis we should expect all four forms to result from each of these combinations in the proportion

T. ar. : T. in. : S. ar. : S. in. : : 9 : 3 : 3 : 1 ;

stating the same result in terms of either character (*i.e.*, colour or fruit form) considered alone, we should expect in each case the ratio 3D : 1R. As regards the results actually obtained, it will be seen that they accord with expectation in so far that all four types appeared in each set of unions, and that in every case Tatula plants were more numerous than Stramonium, and armed than unarmed; on the other hand, the total number of Stramonium plants somewhat exceeds that demanded by the theory, while that of the wholly recessive and least frequently occurring form S. in. is considerably below the calculated result. In considering the former discrepancy it should, however, be borne in mind that any errors in the classification of the many seedlings which perished early would all tend in the same direction, viz., to increase the Stramonium totals, since in the youngest seedlings the tinge of red is sometimes so faint that it may occasionally have escaped notice altogether; and regarding the latter, that in many cases the number of Stramonium plants which lived to maturity was decidedly small.

In the results recorded in Tables IX, X, and XI we have a much closer agreement with Mendel's ratio. Many of the cross-bred parents here used were among the number of those employed in the preceding experiments, where the expected result was less consistently approached, but there are manifestly more possibilities of fluctuation in the one case than in the other.

(γ.) When the cross-breds are crossed with the original recessive form

Table IX.

Parentage.	Number of seed parents.	Number of flowers.	Number of offspring.					
			Number of seedlings.		Number of plants which matured fruits.			
			T.	S.	T. ar.	T. in.	S. ar.	S. in.
(T. ar. × T. in.) × T. in.	3	3	56 36 19		23 19 8	24 13 11		
		Total	111	0	50	48		
Expected result	..	..	*All T.*		*1*	*1*		
(T. in. × T. ar.) × T. in.	2	2	45 ∞ (Almost all killed by frost)		6 5	7 —		
		Total	?	0	11	7		
Expected result	..	..	*All T.*		*1*	*1*		
(T. ar. × S. in.) × S. in.	6	6	Not recorded		9 8 6 3 1	10 6 6 3 1	8 6 11 5 —	6 7 6 3 2
		Total			27	26	30	24
Expected result	..	..			*1*	*1*	*1*	*1*

(δ.) When the cross-breds are crossed with the original dominant form.

Table X.

Parentage.	Number of seed parents.	Number of flowers.	Number of offspring.					
			Number of seedlings.		Number of plants which matured fruits.			
			T.	S.	T. ar.	T. in.	S. ar.	S. in.
(T. in. × T. ar.) × T. ar.	1	1	27		23			
Expected result	..	..	*All T.*		*All ar.*			
(S. in. × S. ar.) × S. ar.	1	1		51			34	
Expected result	..	..		*All S.*			*All ar.*	
(S. in. × T. ar.) × T. ar.	1	1	79		29			
Expected result	..	..	*All T.*		*All ar.*			

(ε.) When the cross-breds, whose parents each combined one dominant with one recessive character, are crossed with one of the parent forms.

Table XI.

Parentage.	Number of seed parents.	Number of flowers.	Number of offspring.					
			Number of seedlings.		Number of plants which matured fruits.			
			T.	S.	T. ar.	T. in.	S. ar.	S. in.
(T. in. × S. ar.) × S. ar.	3	3	59 103 7	51 108 8	3 9 6		3 7 7	
		Total	169	167	18	0	17	0
Expected result	..	..	*1*	*1*	*All ar.*		*All ar.*	

III. *Subsequent Generations.*

Case 1. Parentage [(T. ar. × S. in.) × Self] × Self.

Assuming that Mendel's law holds,

T. ar. × S. in. gives all T. ar., impure, because

any such cross-bred (T. ar.) × Self gives a mixed offspring in the proportions 9 T. ar., 3 T. in., 3 S. ar., 1 S. in.

But of sixteen such individuals only one of each kind (four in all) is pure, yielding its like and only its like when self-fertilised; from each of the twelve remaining plants (when self-fertilised) more than one type will be obtained. For

the 9 apparent T. ar. plants represent 4 different kinds of individuals, viz.:—

- (*a*) 1 pure T. ar., yielding only T. ar.; indicated by the expression T. ar. (T. ar.).
- (*b*) 2 impure T. ar., yielding T. ar. and T. in. in the ratio of 3 : 1; indicated by the expression T. ar. (T. in.).
- (*c*) 2 impure T. ar., yielding T. ar. and S. ar. in the ratio of 3 : 1; indicated by the expression T. ar. (S. ar.).
- (*d*) 4 impure T. ar., yielding T. ar., T. in., S. ar., S. in., in the ratio of 9 : 3 : 3 : 1 indicated by the expression T. ar. (S. in.).

the 3 apparent T. in. plants represent 2 different kinds of individuals, viz.:—

- (*e*) 1 pure T. in., yielding only T. in.; indicated by the expression T. in. (T. in.).
- (*f*) 2 impure T. in., yielding T. in. and S. in. in the ratio of 3 : 1; indicated by the expression T. in. (S. in.).

the 3 apparent S. ar. plants represent 2 different kinds of individuals, viz.:—

- (*g*) 1 pure S. ar., yielding only S. ar.; indicated by the expression S. ar. (S. ar.).
- (*h*) 2 impure S. ar., yielding S. ar. and S. in. in the ratio of 3 : 1; indicated by the expression S. ar. (S. in.).

the 1 S. in. is pure, yielding only S. in., indicated by the expression S. in. (S. in.).

Thus it is obvious that only in the case of those among the offspring of cross-breds (self-fertilised) which exhibit both recessive characters is it possible to know, without further experiment, with exactly what kind of individual one is dealing. In the following experiment a single flower was self-fertilised on each of eight individuals selected at random from among the offspring of cross-breds, viz., 3 T. ar., 4 T. in., and 1 S. ar. The results tabulated below afford a striking illustration of the Mendelian principle.

Plant.	Type.	Number of seedlings.		Number of plants which matured fruits.				Conclusions.
		T.	S.	T. ar.	T. in.	S. ar.	S. in.	
A	T. ar.	56		17	6			∴ A = T. ar. (T. in.)
B	,,	42	15	32		7		,, B = T. ar. (S. ar.)
C	,,	235	80	11	4	3	2	,, C = T. ar. (S. in.)
D	T. in.	27			10			,, D = T. in. (T. in.)
E	,,	15			4			,, E = T. in. (T. in.) probably
F	,,	23	7		20		5	,, F = T. in. (S. in.)
G	,,	8	2		8		1	,, G = T. in. (S. in.)
H	S. ar.		19			11	6	,, H = S. ar. (S. in.)

Case 2. Parentage [(T. ar. × S. in.) × S. in.] × Self.

In this case we should expect to find that only four kinds of individuals would occur among the offspring of the cross-breds (T. ar. × S. in.) resembling in appearance the four type forms, and therefore that all those of similar appearance would give similar results as follows :—

Any T. ar. would yield a mixed offspring in the proportions 9 T. ar., 3 T. in., 3 S. ar., 1 S. in. ; ∴ T. ar. (S. in.).

Any T. in. would yield a mixed offspring in the proportions 3 T. in., 1 S. in. ; ∴ T. in. (S. in.).

Any S. ar. would yield a mixed offspring in the proportions 3 S. ar., 1 S. in. ; ∴ S. ar. (S. in.).

Any S. in. would yield a pure offspring all S. in. ; ∴ S. in. (S. in.).

A single flower was self-fertilised on each of five individuals among the offspring of the cross-breds, viz., 1 T. ar., 1 T. in., 2 S. ar., 1 S. in., and the anticipated result was obtained.

Plant.	Type.	Number of seedlings.		Number of plants which matured fruits.				Conclusions.
		T.	S.	T. ar.	T. in.	S. ar.	S. in.	
I	(T. ar.)	Many	Few	6	1	5	1	∴ I = T. ar. (S. in.)
J	(T. in.)	71	23		38		19	,, J = T. in. (S. in.)
K	(S. ar.)		120			27	10	,, K = S. ar. (S. in.)
L	(S. ar.)		153			34	12	,, L = S. ar. (S. in.)
M	(S. in.)		27				20	,, M = S. in. (S. in.)

Case 3. Parentage [(T. ar. × S. in.) × S. in.] × S. in.

The offspring of any individual (T. ar. × S. in.) × S. in. should in this case exhibit the same number of forms as the offspring of any individual of similar appearance in the preceding experiment, but in the ratio, when mixed, of 1 : 1, instead of 3 : 1. The qualitative result was obtained, and, considering the small totals, the numbers may reasonably be taken to indicate a quantitative agreement also.

Plant.	Type.	Number of seedlings.		Number of plants which matured fruits.				Conclusions.
		T.	S.	T. ar.	T. in.	S. ar.	S. in.	
L	(S. ar.)		124			23	18	∴ L = S. ar. (S. in.)
N	(S. in.)		115				42	,, N = S. in. (S. in.)
O	(T. ar.)	43	35	15	11	9	18	,, O = T. ar. (S. in.)

Case 4. Parentage [(T. in. × S. ar.) × S. ar.] × Self.

Among the offspring of (T. in. × S. ar.) × S. ar., we find two forms only, viz., T. ar. and S. ar., but we may expect each form to include two kinds of individuals; there would thus be four kinds of individuals in all, of which one alone would be pure, and three impure, viz.,

(1) T. ar. yielding a mixed offspring in the proportions 9 T. ar., 3 T. in., 3 S. ar., 1 S. in.; ∴ T. ar. (S. in.).

(2) T. ar. yielding a mixed offspring in the proportions 1 T. ar., 1 S. ar.; ∴ T. ar. (S. ar.).

(3) S. ar. yielding a mixed offspring in the proportions 1 S. ar., 1 S. in.; ∴ S. ar. (S. in.).

(4) S. ar. yielding a pure offspring all S. ar.; ∴ S. ar. (S. ar.).

The nine individuals selected at random, viz., 4 T. ar. and 5 S. ar. justified expectation.

Plant.	Type.	Number of seedlings.		Number of plants which matured fruits.				Conclusions.
		T.	S.	T. ar.	T. in.	S. ar.	S. in.	
P	(T. ar.)	72	20	65		18		∴ P = T. ar. (S. ar.)
Q	,,	100	30	45	14	14	5	,, Q = T. ar. (S. in.)
R	,,	43	19	20	7	8	5	,, R = T. ar. (S. in.)
S	,,	58	17	30	7	12	5	,, S = T. ar. (S. in.)
T	(S. ar.)		115			85		,, T = S. ar. (S. ar.)
U	,,		13			10		,, U = S. ar. (S. ar.)
V	,,		22			17		,, V = S. ar. (S. ar.)
W	,,		193			69		,, W = S. ar. (S. ar.)
X	,,		366			204	50	,, X = S. ar. (S. in.)

Case 5. Parentage [(T. in. × S. ar.) × S. ar.] × S. ar.

Five of the individuals used in the preceding experiment, viz., P, Q, R, T, U, were crossed with the pure form S. ar.; from T. U, the offspring would presumably be all S. ar., while from P, Q, and R alike, if the conclusions stated above are correct, we should expect the result 1 T. ar. : 1 S. ar. From each individual a result in accord with the expectation was obtained.

Plant.	Type.	Number of seedlings.		Number of plants which matured fruits.			
		T.	S.	T. ar.	T. in.	S. ar.	S. in.
P	(T. ar.)	68	74	45		52	
Q	(T. ar.)	67	58	40		35	
R	(T. ar.)	49	55	33		36	
	Total ..	184	187				
T	(S. ar.)		110			76	
U	(S. ar.)		69			63	
	Total ..	0	179				

From the various results detailed above we may conclude that, as in Lychnis, and probably also in Atropa, we have obedience to the Mendelian law in the case of a single pair of antagonistic characters, so in Datura we have a similar result for the more complicated case in which two such pairs of characters are concerned.

MATTHIOLA.

Various races of stocks were employed, differing in regard to the character of the leaf-surface, colour of seeds, colour of flowers, and the time of flowering. It was found that the results differed widely according to the variety, and occasionally according to the individual, with which the crosses were made. These differences are highly complex, and in some cases altogether unexpected. After every effort at clearness in arrangement and tabulation, the statement of results remains complicated and difficult to follow.

List of Types used and their Characters.

The various races of stocks* employed differed in regard to

Habit, whether annual or biennial.
Character of leaf surface, whether hoary or glabrous.
Colour of flowers, various.†
Colour of seeds, whether green, brown, or intermediate.

Type 1. Biennial; leaves hoary; flowers white;‡ seeds black in outward appearance, this colour being due to green colour in the embryo overlaid with a violet layer; obtained from a coast-guard station in the Isle of Wight, and probably derived from the wild *M. incana.*

Type 2. Annual; leaves hoary on *under* surface, but glabrous, or nearly so, on the *upper* surface, a condition hereafter called "half-hoary"; flowers white; seeds yellowish brown; from same locality as Type 1. Origin unknown.

Type 3. Annual "ten-week" stocks; leaves hoary; flowers white;

- *3a.* Seeds yellowish brown; kindly obtained by Mr. Lynch from the Royal Gardens, Kew.
- *3b.* Seeds yellowish brown (commercial seed).
- *3c.* Seed colour unknown, plants found in a Cambridge garden.

Of these three forms the first two, *3a* and *3b*, were indistinguishable in appearance, but behaved differently in crossing. Of *3c* very little was known.

Type 4. Annual "ten-week" stock; leaves hoary; flowers purple; seeds green (commercial seed).

Type 5. Annual "ten-week" stocks; leaves glabrous;§

5a.	Flowers white.	Seeds yellowish brown.
5b.	,, cream or yellowish white.	
5c.	,, red.	
5d.	,, pinkish white.	
5e.	,, bluish pink.	

(Commercial seed.)

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* Only single-flowered plants were chosen to breed from in any of these experiments. Doubles constantly presented themselves, but variations in respect of this character were not considered. Records were kept, but are not included in this paper. The same is true regarding the order of flowering of the axes. The character, width of seed-wing, used by Correns, was not studied.

† Unfortunately we have not yet fully identified the colour varieties according to the seedsmen's lists. Messrs. Haage and Schmidt have kindly supplied us with a set of their varieties, and from the descriptions and seed-characters we do not doubt that our "cream" is their "sulphur-yellow."

‡ In 1901 the flowers of this form were faintly tinged with purple.

§ In these forms the absence of hairs is absolute in many individuals, but in some cases a single hair or group of hairs may occur at the extreme apex of the leaf. The cotyledons of *all* types, whether glabrous or hoary, are invariably glabrous.

Type 6. Annual "ten-week" stocks; leaves glabrous;[‡]

6*a*. Flowers light purple.
6*b*. " dark purple.
6*c*. " claret coloured.
6*d*. " lilac.
Seeds green.
(Commercial seed.)

Type 7. Biennial "Brompton" stocks; leaves hoary; flowers white; seeds intermediate in colour, becoming much yellower on keeping.

7*a*.
7*b*.
7*c*.
Samples from various sources. 7*b* was represented by a single plant.

Type 8. Biennial "Brompton" stocks; leaves hoary; flowers reddish purple; seeds green.

8*a*.
8*b*.
8*c*.
Various plants of unknown origin which gave results not wholly uniform.

With the exception of 3*c*, 4, 7, and 8, which were not tested, all these varieties have been found to breed truly on self-fertilisation.

The colour of the seeds was found to be due to two distinct factors: to the colour of the embryo, and also to that of the testa—a structure belonging to the mother-plant—through which the embryo is seen. The testa though shading from lemon-yellow through bright-yellow to light-brown was always of this one class of colour, and as a rule of sufficient transparency to allow one to judge whether the colour of the underlying embryo was yellowish, or more or less deep green or green tinged with violet. It was therefore generally possible to classify the unskinned seeds; but in cases in which a more or less continuous series of tints was obtained it was not always easy to decide where to draw the dividing line, and in these instances sorting was not attempted. Consequently, the classification of seeds into brown and green is to be taken as indicating differences in the embryos. When seeds are described as of intermediate tint, it is not certain whether the embryo was greenish or truly intermediate, but in no such case would the embryo be the true yellow of the types. The only type which had a normally intermediate seed was 7.

In embarking on these experiments it was originally intended to investigate statistically the laws of inheritance operating in regard to hoariness and glabrousness. Experiment, however, soon revealed the fact that the results in regard to this specified character differed greatly according as one or other of the several varieties was used, and it became necessary to investigate also the properties of the other differentiating characters in their various combinations.

I. *First Cross-bred Generation.*

A. *Details as to Offspring of Hoary × Glabrous.* (*Table I.*)

From Table I it appears that when the hoary forms are employed as seed-parent, the hoary character is, except in one union (Experiment 10), completely dominant. Of about a 1000 individuals raised from such crosses between various hoary and glabrous strains, all were hoary. It is noticeable that when the form No. 2, which has only the underside of the leaves hoary ("half-hoary") was used, *the resulting plants were completely hoary like those bred from a completely hoary parent.* To this statement two individual offspring, which came of the half-hoary type, were the only exceptions out of more than 100 plants thus raised.

The exception to the rule of universal appearance of the hoary character is found in Experiment 10. In this experiment two sister plants belonging to the half-hoary type (2) when crossed with the glabrous form (5*a*) produced seventy-two plants all glabrous, although when crossed with another glabrous strain (6*c*) the same two individuals gave the usual result (Experiment 11). Now the sister plants were descended by two generations of self-fertilisation from a common grandparent, and both the glabrous strains with which they were crossed had also been raised by two successive self-fertilisations. Both the parent and the grandparent of the two half-hoary plants had, when crossed with the glabrous strains 5*b* and 6*a* respectively (see Experiments 7 and 1), produced the hoary form and the hoary form only, but whether the unusual result in the third generation is in any degree to be attributed to repeated self-fertilisation, the evidence to hand is not yet sufficient to determine. As against such a view, however, we have the result obtained in the experiment with the other glabrous form 6*c* (Experiment 11), in which no such effect was produced.

As regards seed-colour, green appears usually to be a dominant, brown a recessive character; but the intensity of the green colour may become so much diminished on crossing, that when seen through the brown testa, the net result may be a more or less intermediate tint.

As regards flower-colour the results were far more complex, the product of combinations of *identical* colours varying according to the particular strain employed. It will therefore be more convenient to treat the question of flower-colour when the results of the crosses glabrous × hoary detailed in Table II have also been considered.

B. *Details as to Offspring Glabrous × Hoary.*

From Table II it will be seen that in ten out of the fourteen fruits obtained in the first year (1897–8), from a cross between a *brown* seeded glabrous type and the *black* seeded hoary type 1 (Experiments

Table I.—Offspring obtained from the cross Hoary ♀ × Glabrous ♂.

Number of experiment.	Date.	Parentage.	Number of seed parents.	Number of flowers.	Colour of resulting seeds.	Number of offspring.			Colour of corolla in offspring.†
						Hoary.	Inter. *	Glabrous.	
1	1897–98	2 × 6*a* ½*H. wh. br.* × *G. lp. gr.*	2	3	Green	34	—	—	Medium purple.
2	..	2 × 5*c* ½*H. wh. br.* × *G. r. br.*	2	3	Brown	16	—	—	Pink.
3	..	3*a* × 5*c* *H. wh. br.* × *G. r. br.*	2	2	Greenish	30	—	—	Medium purple.
4	..	3*b* × 5*c* *H. wh. br.* × *G. r. br.*	4	5	Brownish or greenish	48	—	—	Pink.
5	..	3*b* × 6*b* *H. wh. br.* × *G. dp. gr.*	2	2	Green	4	—	—	Medium purple.
6	..	3*b* × 6*c* *H. wh. br.* × *G. cl. gr.*	4	4	Green	21	—	—	Medium purple.
7	1898–99	(2 × self) × (5*b* × self) ½*H. wh. br.* × *G. cr. br.*	1	1	Brown	47	1	—	Pink.
8	..	(2 × self) × (6*c* × self) ½*H. wh. br.* × *G. cl. gr.*	1	1	Greenish	9	—	—	
9	..	(3*b* × self) × (5*b* × self) *H. wh. br.* × *G. cr. br.*	1	1	Brown	2	—	—	
10	1899–1900	[(2 × self) × self] ½ *H. wh. br.* × [(5*a* × self) × self] *G. wh. br.*	2	3	Brown	—	—	72	
11	..	× [(6*c* × self) × self] *G. cl. gr.*		3	Green and brownish	117	1	—	Bluish pink.

* Under the head "intermediate" are included all plants resembling type No. 2, or exhibiting any lesser degree of hoariness; since in such of the latter as were allowed to flower the calyx and ovary were always hoary, it is evident that these individuals are more correctly to be added to the hoary than to the glabrous columns in the statement of totals.

† When no colour is given for the corolla the plants were destroyed before flowering.

Number of experiment.	Date.	Parentage.	Number of seed parents.	Number of flowers.	Colour of resulting seeds.	Number of offspring.			Colour of corolla in offspring.
						Hoary.	Inter.	Glabrous.	
12	1899–1900	[(3*b* × self) × self] × [(5*a* × self) × self] *H. wh. br.* × *G. wh. br.*	4	6	Green and few brown	194	—	—	Light purple.
13	..	[(3*b* × self) × self] × [(5*b* × self) × self] *H. wh. br.* × *G. cr. br.*	1	1	Inter.	3	—	—	Pink.
14	..	[(3*b* × self) × self] × [(6*c* × self) × self] *H. wh. br.* × *G. cl. gr.*	2	2	Green and greenish	13	—	—	Medium purple.
15	1900–01	1 × 5*b* *H. wh. bl.* × *G. cr. br.*	4	20	Green	371	—	—	
16	..	1 × 5*c* *H. wh. bl.* × *G. r. br.*	4	15	Green	119	—	—	
17	..	1 × 5*d* *H. wh. bl.* × *G. pk. wh. br.*	4	6	Green	77	—	—	
18	..	1 × 6*b* *H. wh. bl.* × *G. dp. gr.*	3	8	Green	145	—	—	

ABBREVIATIONS USED IN THE TABLES TO DENOTE LEAF-CHARACTER, FLOWER-COLOUR, AND SEED-COLOUR.

LEAVES.—H, hoary; $\frac{1}{2}$H, half-hoary; G, glabrous.

FLOWERS.—cl., claret; cr., cream; li., lilac; bl. pk., bluish pink; p., purple; dp., dark purple; mp., medium purple; lp., light purple; rp., reddish purple; r., red; wh., white; pk. wh., pinkish white.

SEEDS.—bl., black; br., brown; gr., green; in., intermediate.

Table II.—Offspring obtained from the cross Glabrous ♀ × Hoary ♂.

Number of experiment.	Date.	Parentage.	Number of seed parents.	Number of flowers.	Colour of resulting seeds.			Number of offspring.		Colour of corolla in offspring.	
					Green.	Inter.	Brown.	Hoary.	Glabrous.	Hoary.	Glabrous.
19	1897–98	5*a* × 1 *G. wh. br.* × *H. wh. bl.*	1	1	All	—	—	16	—	Dark purple	
20	"	5*b* × 1 *G. cr. br.* × *H. wh. bl.*	1	2	All	—	—	23	—	"	
			1	2	All	—	—	19	—	"	
				1	30 (24 sown)	17	5	21	—	"	
								—	14		Cream.
								—	2		Cream.
*20	1900–01	" "	1	6	All	—	—	63	—		
21	1897–98	5*c* × 1 *G. r. br* × *H. wh. bl.*	1	2	All	—	—	11	—	"	
*21	1900–01	" "	1	8	All	—	—	13	—		
22	1897–98	5*d* × 1 *G. pk. wh. br.* × *H. wh. bl.*	1	1	All	—	—	14	—	Medium purple	
				1	30	1	6	26	—	"	
								—	1		Pinkish.
								—	6		Pinkish.
			1	1	48 (12 sown)		3	10	—	"	
				1	37 (28 sown)	4		25	—	"	
								2	—	Produced no flowers	
*22	1900–01	" "	1	2	All	—	—	23	—		

Number of experiment.	Date.	Parentage.	Number of seed parents.	Number of flowers.	Colour of resulting seeds.			Number of offspring.		Colour of corolla in offspring.	
					Green.	Inter.	Brown.	Hoary.	Glabrous.	Hoary.	Glabrous.
23	1897-98	5e × 1 *G. bl. pk. br.* × *H. wh. bl.*	1	1	All ?	—	—	13	—	Medium purple	
				1	45 (26 sown)		6 (4 sown)	23 —	— 4	”	Bluish pink.
24	”	6a × 1 *G. lp. gr.* × *H. wh. bl.*	1	2	All (24 sown)	—	—	8	—	Light purple	
25	”	6b × 1 *G. dp. gr.* × *H. wh. bl.*	1	1	All (12 sown)	—	—	12	—	Dark purple	
*25	1900-01	” ”	1	4	All	—	—	20	—		
				5	All	—	—	71	18		
26	1897-98	6c × 1 *G. cl. gr.* × *H. wh. bl.*	1	1	All	—	—	21	6	Dark purple	Claret.
27	”	6d × 1 *G. li. gr.* × *H. wh. bl.*	1	1	All	—	—	22	—	Light purple	
28	”	6c × 3a *G. cl. gr.* × *H. wh. br.*	1	1	All	—	—	11	—	Pink	
29	”	6d × 3a *G. li. gr.* × *H. wh. br.*	1	1	All	—	—	14	—	Light purple	

19—23 without asterisks) the seeds were uniform in colour (green), and sample sowings yielded hoary plants only. In the four remaining fruits borne by some of the same individuals (Experiments 20 and 22) the seeds were mixed—green, intermediate (the embryos being either yellowish green, or green with yellow radicles), and brown—and gave rise to a mixed offspring. These green seeds, like those from fruits with green seeds *only*, gave rise to hoary plants, the brown seeds to glabrous plants, and the intermediates to both forms. In these experiments the hoary parent was *white* flowered. The glabrous parent was *either white, cream, red, or pinkish.* Nevertheless, irrespective of the colour introduced by the glabrous parent, all the *hoary* offspring were *purple* without exception. The glabrous offspring, however, invariably exhibited the colour of their glabrous parent.

When one individual belonging to each of the four *green* seeded glabrous strains was crossed with the same *black* seeded hoary type 1 (Experiments 24—27 without asterisks), the resulting seeds were of one type of colour, either pure or rusty green, and afforded no indication as to the nature of the future plants. A full sowing from one individual, and sample sowings from two others, produced forty-two plants all hoary; from the remaining individual a mixed offspring was obtained, in which as before the colour of the flowers of the glabrous plants resembled that of the glabrous parent. The hoary cross-breds were all purple-flowered.

Lastly from a cross (Experiments 28—29) between two of the same *green* seeded glabrous strains and a *brown* seeded hoary form, green seeds and hoary plants alone were obtained, although one of the glabrous parents was the identical individual which gave the mixed offspring when crossed with the hoary type No. 1. So far as this result can be regarded as conclusive (only twenty-five plants were raised), the dominance of the leaf-character and the seed-colour in this case appears to be complete.

The occurrence of a mixed (hoary and glabrous) offspring in the first cross-bred generation, as has been stated above, had been previously observed by Trevor Clarke in cases in which the glabrous form was used as the seed parent (see p. 13). The actual numbers, however, are not given by him, nor is it stated whether the mixture occurred in the case of every flower or even of every individual. As in our own experiments the mixed result was constant neither for all the individuals of one strain, nor for the different flowers on a single individual, it was proposed to repeat this experiment in the following year. Unfortunately no plants of the original hoary form type 1 survived the winters of 1898 and 1899, and as this species does not flower in its first season, it was impossible in these two years to repeat precisely the original crosses. Recourse was therefore had to such hoary Brompton stocks or other strains as were available at the moment. The glabrous parents were in each case descendants (by self-fertilisation) of the original plants.

In these unions of 1898–1900 (Table III), the occurrence among the offspring of a larger or smaller number of recessives (glabrous) was the rule rather than the exception. Complete prevalence of the hoary character was only obtained in the four experiments (30—33) in which the hoary parent was a purple-flowered Brompton stock, and in two out of the three cases in which the white-flowered Brompton form, 7*c*, was employed (Experiments 37 and 45). In the remaining cross with 7*c*, in all those with the other white-flowered Bromptons 7*a* and 7*b*, with the white-flowered annual 3*c*, and with the purple-flowered annual 4, the offspring included some recessives. Reference to the table, however, will show that in those cases in which the offspring were mixed, the mixed result was not given by every seed parent employed, but by particular individuals or even, indeed, by particular flowers. For in some cases in which several flowers on the same individual were crossed, the offspring of some were mixed and of others not. It is not surprising therefore that when the totals obtained in the different unions are compared, no constant proportion between the two characters is discoverable. So far, however, the irregularity of these results remains unexplained.

In regard to seed-colour, in the four experiments (42—45), where *green*-seeded glabrous strains were crossed with the white-flowered Bromptons (seeds intermediate) the results varied; twice the seeds were all green, once mixed, and once difficult to classify. When *brown*-seeded glabrous strains were crossed with the same white Bromptons (Experiments 35—41) the resulting seeds were never uniformly coloured, though occasionally all those in a single fruit were alike. Nevertheless, a comparison of the numbers failed to reveal any constant proportion between the various seed-colours. In the cases in which brown-seeded glabrous strains were crossed with purple-flowered forms (seeds green) we find the same irregular result as before in the cross with the annual type 4 (Experiment 34), but with the Brompton strains the case is very different (Experiments 30—32). In the unions with 8*b* and 8*c*, the green colour was completely dominant, with 8*a* equal numbers of brown and green seeds were produced, the colours being well-marked and without intermediates. This equality in the totals was further borne out by the figures obtained for each individual, but it is of interest to note that a similar uniformity of distribution did not always extend to the separate flowers. Although, as a matter of fact, every cross-bred fruit contained both seed forms, yet in some there were only one or two of one or other colour.

The occurrence here of both seed-colours recalls the mixed result obtained in some cases in the preceding year with the hoary type No. 1. In those cases, however, there was no constant proportion

Table III.—Offspring obtained from the cross Glabrous ♀ × Hoary ♂.

In these experiments the seed-parent was the result of one or two self-fertilisations.

No. of expt.	Date. 1898—99, 1899—1900	Parentage.	Number of seed parents.	Number of flowers.	Colour of resulting seeds.			Number of offspring.*		Colour of flower in offspring.	
					Green.	Interm.	Brown.	Hoary.	Glabrous.	Hoary.	Glabrous.
30	..	(5*b* × self) × 8*a* *G. cr. br.* × *H. rp. gr.*	8	4	105		101	98	—	Purple Red	
				2	46		57	83	—		
				4	99		89	45	—		
				2	51		59	46	—		
				2	21		20				
				4	49		55				
				2	40		37				
				1	4		8				
		Total....	8	21	425	—	426	272	—		
31	..	[(5*b* × self) × self] × 8*b* *G. cr. br.* × *H. rp. gr.*	4	4	All	—	—	26	—	Purple	
32	..	[(5*a* × self) × self] × 8*c* *G. wh. br.* × *H. rp. gr.*	2	2	All	—	—	27	—	Purple	
33	..	[(6*c* × self) × self] × 8*b* *G. cl. gr.* × *H. rp. gr.*	2	2	All	—	—	39	—		
34	..	[(5*a* × self) × self] × 4 *G. wh. br.* × *H. p. gr.*	1	1	1	14	24	15	22	Purple	White
35	..	(5*b* × self) × 7*a*	8	19	221	71	331	332	—		

			3	1 12	— 65	— —	35 484	34 260	1 16	Red	Cream
		Total....	12	35	294	146	850	672	17		
36	..	(5*b* × self) × 7*b* *G. cr. br* × *H. wh. in.*	1	1	3	17	11	13	8		Cream
37	..	[(5*b* × self) × self] × 7*c* *G. cr. br.* × *H. wh. in.*	2	5	93	71	65	155	—	Pink	
38	..	(5*a* × self) × 7*a* *G. wh. br.* × *H. wh. in.*	1	3	95	—	7	92	7	Purple	
39	..	(5*a* × self) × 7*b* *G. wh. br.* × *H. wh. in.*	7	18	483	34	63	440	27	Purple	
40	..	[(5*a* × self) × self] × 7*c* *G. wh. br.* × *H. wh. in.*	2	2	2	49	8	50	7		
41	..	(5*d* × self) × 7*a* *G. pk. wh. br.* × *H. wh. in.*	3	8	—	26	235	236	11	Pink	Pinkish white
42	..	(6*c* × self) × 7*a* *G. cl. gr.* × *H. wh. in.*	6	21	All	—	—	382	44	Purple	—
43	..	(6*c* × self) × 7*b* *G. cl. gr.* × *H. wh. in.*	3	12	∝		 39	339 —	17 38	Purple	 Claret
		Total....	3	12	∞	—	39	339	55		
44	..	(6*b* × self) × 7*b* *G. dp. gr.* × *H. wh. in.*	1	1	All	—	—	31	8		
45	..	[(6*c* × self) × self] × 7*c* *G. cl. gr.* × *H. wh. in.*	3	3	Not classified			71	—		
46	..	[(5*b* × self) × self] × 3*c* *G. cr. br.* × *H. wh.* ?	2	2	96	2	4	33	4	Purple	Cream
47	..	[(5*a* × self) × self] × 3*c* *G. wh. br.* × *H. wh.* ?	2	2	59	—	4	57	2	Purple	White
48	..	[(6*c* × self) × self] × 3*c* *G. cl. gr.* × *H. wh.* ?	1	1	All	—	—	6	5	Purple	Claret

Generally speaking, when the seeds were mixed and gave rise to mixed plants, the glabrous plants arose from brown seeds.

* In this and all succeeding tables a blank space opposite the seed numbers indicates that these seeds were not sown.

between the two colours, and, on the other hand, brown seed-colour was correlated with glabrous leaf-character. It should, however, be stated that the seed-*colour* purity of the type 8*a* was not separately tested, as was done in the case of type 1, and that the production of *equal* numbers of the two seed-colours is precisely the result which we should expect if 8*a* were not a pure colour form, but itself a cross-bred in this respect. This possibility cannot now be disproved; but it may be noted that Trevor Clarke obtained a like result from a cross between a brown-seeded and a black-seeded form, 50 per cent. of the seeds coming black.

Finally in the remaining union (Experiment 33), in which both parents were green seeded, the resulting seeds were all green.

A further attempt to obtain confirmation of these results was made, especially in view of the appearance at this point of Correns'* "Levkojenbastarde." Commenting upon Trevor Clarke's results, which are at variance with his own observations regarding the complete dominance of the hoary character, he suggests that the occurrence of a mixed offspring in the first generation is to be attributed to subsequent (? self) fertilisation. Such an explanation, however, takes no account of the alteration in habit of the glabrous plants which Trevor Clarke describes, a fact which would seem to vindicate the accuracy of his experiments.† It seems equally unlikely that the exceptions to the universal appearance of the hoary character observed in our own experiments are to be attributed to experimental error; for it is difficult to believe that in cross-fertilisations with, *e.g.*, white-flowered and purple-flowered Brompton strains, carried out at the same time, and sometimes upon the same individuals, an error should frequently occur in the former unions and never in the latter. As, however, some more plants of the hoary type No. 1 had in the meantime been successfully raised, an exact repetition of the original experiment was now performed with the added precaution that in the case of the glabrous parents all unemasculated flower-buds were removed before the dehiscence of the anthers. (Experiments marked with *, Table II.) In this way any possibility of error arising from the presence of thrips or other insect too minute to be excluded by the muslin cover, which might carry pollen from one flower to another, was avoided.

Once again a confirmation of the earlier results was obtained, for in one of the unions (6*b* × 1, Experiment 25*), in which several flowers on one individual had been crossed, some of the cross-bred fruits yielded a mixed offspring, while from others hoary plants only were obtained.

From the sum of these results it is evident that in the cross glabrous × hoary, the hoary character appears in the offspring in the vast majority of cases; but further experiments are needed in order to determine how far we are here dealing with a question of strain, of the individual, or even of separate flowers, or to what extent, if any, these results are dependent upon varying conditions.

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* 'Bot. Cblt.,' 1900, vol. 84.

† Unfortunately, in the similar cases herein described, no reliable observations on this question of habit were recorded.

Subsequent experiments, which will be set forth in detail hereafter, showed that the constitution of the dominant offspring, produced in these crosses, differed radically from that of the recessives. For while the former (hoary) were proved to give rise to mixed offspring in fair accordance with Mendelian expectation, the latter (glabrous) *behaved as pure glabrous forms, giving rise to glabrous offspring only, when self-fertilised.*

This phenomenon is discussed hereafter in connection with others of a like nature (p. 154).

C. *Flower-colour of First Cross-bred Generation.*

To return to the question of flower-colour, the results in both sets of experiments (A and B) may be most easily gathered from the following schedule, in which the various unions giving an identical result are grouped together in each column.

In regard to the recessive offspring such a schedule is unnecessary, since in each case the flower-colour of recessive offspring resembles that of the recessive parent, though whether the shade was identical in all cases is not certain.

In the table (p. 46), the crosses hoary × glabrous and glabrous × hoary have been separated for convenience of reference, but there is no reason to suppose any significance (in regard to flower-colour) to attach to the circumstance of the way the cross was made. Flower-colour was not a primary subject of these experiments, and, as it happens, no true reciprocals were flowered.

The coloured forms red, pink, purple, claret, have not yet been crossed *inter se.*

In each case one parent was white, except in one instance when cream was crossed with purple (13). *No white* offspring were produced in first crosses. In some cases there was obvious blending, as for example when white crossed with red or claret, gave pink. More often the result was a wholly new colour, and except in four cases (6, 9, 27, 13*b*), always some shade of purple, but varying in tint even in crossings of similar colours according to the particular strains employed. Not only are such purple offspring produced when some of the coloured forms are crossed with white, but even in the crosses *between two distinct white forms* (10, 19, 24). Possibly we have here a reappearance of the colour commonly occurring in the wild species (*incana*), from which the hoary garden stocks may have originated—a case in fact of "reversion" (see p. 144). In the four exceptions 6, 9, 27, 13*b*, in which cream was

Colours of Flower in DOMINANT *Cross-breds.*

Form of union : Hoary × Glabrous.

Dark purple.	Medium purple.	Pale purple.	Pink.	Red.
	(1) white 2 × pale purple 6*a*		(5) white 2 × red 5*c*	
	(2) white 3*a* × red 5*c*		(6) ,, × cream 5*b*	
	(3) white 3*b* × medium purple 6*b*		(7) ,, × claret 6*c*	
	(4) ,, × claret 6*c*		(8) white 3*b* × red 5*c*	
			(9) ,, × cream 5*b*	
Form of union : Glabrous × Hoary.				
(10) white 5*a* × white 1	(17) pinkish white 5*d* × white 1	(21) pale purple 6*a* × white 1	(25) pinkish white 5*d* × white 7*a*	(27) cream 5*b* × white 7*a*
(11) red 5*c* × ,,	(18) bluish pink 5*e* × ,,	(22) lilac 6*d* × ,,	(26) claret 6*c* × white 3*a*	(13*b*) ,, × purple 8*a*
(12) cream 5*b* × ,,	(19) white 5*a* × white 7*a*	(23) ,, × white 3*a*		
(13*a*) ,, × purple 8*a*	(20) claret 6*c* × white 7*b*	(24) white 5*a* × white 7*b*.		
(14) medium purple 6*b* × white 1				
(15) claret 6*c* × ,,				
(16) ,, × white 7*a*				

crossed with white or purple, we have the unexpected appearance of pink or red; a similar occurrence was observed by Correns among the offspring of cross-breds whose parents had "yellowish white" and "violet" flowers respectively.

In connection with the question of colour one point of interest may be briefly mentioned here, viz., the occurrence of "flaking." Although this phenomenon was occasionally observed in the coloured pure strains, even when repeatedly self-fertilised, it was not very common; among the coloured cross-breds, however, it was almost universal. Plants which at first produced exclusively self-coloured flowers, as the season advanced bore flowers speckled or streaked with white. In some cases the last flowers were even entirely white. Such flaking was recorded in thirty-one out of thirty-nine combinations in the first year, and in forty-one out of forty-three in the second.*

D. *Seed-colour of First Cross-bred Generation.*

When brown-seeded and green-seeded types (including "black") were intercrossed, green was generally dominant, though exceptions were seen. When browns were crossed with the intermediate type 7, the results were irregular. Similarly when greens were crossed with these intermediates the results were sometimes irregular. When browns were crossed with browns, the one being glabrous and the other hoary, the result was four times brown, once greenish, once intermediate, and twice a mixture. Green (including "black") with green always gave green.

When in first crosses *glabrous* plants were produced, these arose from seeds similar to those of the glabrous parent, except in one case where the intermediate type 7 was used. In that case glabrous plants came from both *green* and *brown* seeds.

II. *Posterity of Cross-breds.*

The offspring of cross-breds will be described in the following order:—

1. Offspring of cross-breds produced from (D × R).†

   A. *When D and R were brown-seeded and green-seeded respectively.*

      a. When the cross-breds were fertilised with a recessive form. (Table IV.)

      b. When the cross-breds were self-fertilised. (Table V.)

      c. Subsequent posterity derived from the foregoing. (Table VI.)

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* Such flaking is exceedingly common in the *late* flowers of Sweet Peas.

† In what follows, the classification into D, dominant, and R, recessive, refers to the characters hoariness and glabrousness, respectively.

B. *When D and R were both brown-seeded.*

a. When the cross-breds were fertilised with a recessive form. (Table VII.)
b. When the cross-breds were self-fertilised. (Table VIII.)
c. Subsequent posterity derived from the foregoing. (Table IX.)

It was thought desirable to present the set of results contained in A separately from those in B, since the wholly unexpected results obtained in B (section *a*) were absent from the corresponding section in A.

2. Offspring of cross-breds produced from (R × D).

a. When the cross-breds were fertilised with a recessive form. (Table X.)
b. When the cross-breds were self-fertilised. (Table XI.)
c. Offspring of dominant cross-breds produced in 2*a*. (Table XII and Table XIII.)
d. When the cross-breds were fertilised with a dominant form.

Under these heads we have to consider the results of self-fertilising cross-breds (DR × self) and also the results of fertilising cross-breds with recessive (DR × R) and dominant (DR × D) forms. Subsequently we shall have to describe in each case experiments in which offspring so produced were fertilised again with recessives, and so on. To denote the recessive parentage the expressions R_1, R_2, R_3 are employed. In any one expression the numbers denote the order in which distinct recessive strains were introduced into the pedigree.

1. A. *Offspring of Cross-breds (D × R) when D and R were brown-seeded and green-seeded respectively.*

a. *When the Cross-breds were Fertilised with a Recessive Form.*

From Table IV it will be seen that when the cross-breds (2 × 6*a*) were crossed with the recessive form (6*c*) (produced by self-fertilisation), the resulting fruits always contained a mixture of seeds—usually green and dark brown (only in three seeds was the true light-brown of the original parent (type 2) observed); in twenty-two other seeds the colour was difficult to classify. Excluding these last, the total numbers for the two colours are roughly equal, nor is the departure from this result in the case of individuals ever considerable. Each kind of seed gave rise to both forms of plants, and in about equal numbers, the slight deviations in the totals being complementary. In brief, as regards both seed-colour and leaf-surface, we find the Mendelian ratio 1 : 1. The flowers were either bluish-pink or purple, except in two glabrous plants in which they were white becoming tinged later; there appeared to be a well marked though not an absolute correlation between seed- and flower-colour. With few exceptions the pinkish flowers were derived from the brown seeds, and the purple from the green, so that as regards flower-colour the recessive offspring derived from brown seeds more nearly resembled their recessive parent, those from green seeds their more remote recessive progenitor.

In the parallel experiment with (3*b*), the seeds were uniformly coloured (green) but every individual produced a mixed offspring, though the final result (Experiment 50) was rather farther from the ratio 1 : 1.

b. *When the Cross-breds were Self-fertilised.*

The results recorded in Table V were obtained when the identical cross-breds employed as seed parents in Experiment 49 were self-fertilised instead of being crossed with a recessive form. The seeds, more difficult to sort than in the previous case, again showed a rough equality in the two type-colours, but the percentage of intermediates was much greater than before. From each individual and from each kind of seed a mixture of plants was obtained, the green and intermediate seeds giving rise to a majority of hoary, the brown to a majority of glabrous plants. The totals, however, showed a proportion of glabrous plants *far in excess* of the theoretical ratio of 1 : 3.

The above results will be considered in connection with those obtained in the next generation.

Table IV.—Offspring obtained from Fertilising the Cross-breds (D × R) with a Recessive Form, when D and R were brown-seeded and green-seeded respectively.

No. of expt.	Parentage.	No. of seed parents.	No. of flowers.	Colour of resulting seeds.			Number of offspring.			Colour of corolla in offspring.	
				Green.	Inter.	Brown.	Hoary.	Inter.	Glabrous.	Hoary.	Glabrous.
49	(2 × 6*a*) × (6*c* × self) . (½*H.wh.br.* × *G.lp.gr.*) × *G.cl.gr.*	1	2	24			*gr.* 12	—	*gr.* 11	Purple (various)	Purple (various) and pinkish.
						35	*br.* 16	—	*br.* 8	Pinkish except 1 purple	Pinkish except 1 purple.
			1	26			*gr.* 10	—	*gr.* 13	Purple (various)	Purple (various).
					3		*in.* —	—	*in.* 3		
						19	*br.* 12	—	*br.* 7	Pinkish	Pinkish.
		1	2	31			*gr.* 5	—	*gr.* 15	Purple (various)	Purple (various) and pinkish.
						37	*br.* 18	—	*br.* 16	Pinkish	Pinkish.
			2	37			*gr.* 15	—	*gr.* 13		
						39	*br.* 17	*br.* 1	*br.* 13		
		1	2	36			*gr.* 16	—	*gr.* 17	Purple (various)	Purple (various).
						51	*br.* 21	—	*br.* 22	Pinkish	Pinkish.
			1	30			*gr.* 11	—	*gr.* 12		
						24	*br.* 10	—	*br.* 13		
		1	2	38			*gr.* 14	—	*gr.* 15	Purple (various) and pinkish	Purple (various) and pinkish.
						18	*br.* 6	—	*br.* 11	Pinkish	
			2	7			*gr.* 5	—	*gr.* 2	Purple (various)	Purple.
					19		*in.* 8	—	*in.* 7		
						6	*br.* 3	—	*br.* 3		

		1	3	66		62	*gr.* 31	—	*gr.* 31	Purple (various)	Purple (various).
							br. 40	*br.* 2	*br.* 23	—	Purplish-white.
			2	54			*gr.* 27	—	*gr.* 22	Purple (various)	Purple (various) except 1 white.
		1	1	15		41	*br.* 20	—	*br.* 19	Pink (various)	Pink (various).
							gr. 4	—	*gr.* 9		
						15	*br.* 7	—	*br.* 8		
		1	1	26			*gr.* 12	—	*gr.* 14		
						21	*br.* 9	—	*br.* 11		
			1	16			*gr.* 8	—	*gr.* 7		
						14	*br.* 6	—	*br.* 7		
		1	2	56			*gr.* 25	—	*gr.* 31	Purple (var ous)	Purple (various).
						47	*br.* 20	—	*br.* 26	Pinkish	Pinkish.
			2	25			*gr.* 11	—	*gr.* 13	Purple (various)	Purple (various).
						30	*br.* 11	—	*br.* 15	1 pinkish	1 white.
	Total............	8	26	487	22	462	430	3	437		
	$(3b \times 6b) \times (6c \times \text{self})$	1	1	All	—	—	21	—	16		
50	(*H.wh.br.* × *G.dp.gr.*) × *G.cl.gr.*	1	1	,,	—	—	20	—	12		
		1	1	,,	—	—	18	—	14		
		1	2	,,	—	—	50	—	30		
			3	,,	—	—	39	—	47		
		1	1	,,	—	—	14	—	19		
		1	1	,,	—	—	38	—	42		
		1	1	,,	—	—	18	—	17		
		1	4	,,	—	—	90	—	61	Purple (various)	Purple (various).
		1	1	,,	—	—	18	—	24		
		1	1	,,	—	—	8	—	13		
	Total............	10	17	All	—	—	334	—	295		

Table V.—Offspring obtained from the Self-fertilisation of the Cross-breds (D × R), when D and R were brown-seeded and green-seeded respectively.

No. of expt	Parentage.	Number of seed parents.	Number of flowers.	Colour of resulting seeds.			Number of offspring.			Colour of corolla in offspring.		
				Green.	Inter.	Brown.	Hoary.	Inter.	Glabrous.	Hoary.	Inter.	Glabrous.
51	(2 × 6*a*) × self (½ *H. wh. br.* × *G. lp. gr.*)	1	3	36	51	30	*gr.* 22 *in.* 32 *br.* 9	— *in.* 1 *br.* 5	*gr.* 13 *in.* 15 *br.* 16	Purple and Purplish-white. Purple and Purplish-white.		
		1	4	56	62	55	*gr.* 25 *in.* 30 *br.* 10	— — *br.* 6	*gr.* 8 *in.* 15 *br.* 13	As the cross-bred and its recessive parent were both purple, there is no clear indication how the flower-colour descended. Absence of pure whites should be noted.		
		1	3	58	38	41	*gr.* 39 *in.* 24 *br.* 6	— *in.* 1 —	*gr.* 5 *in.* 11 *br.* 32			
		1	6	71	58	58	*gr.* 34 *in.* 39 *br.* 6	— *in.* 2 —	*gr.* 20 *in.* 10 *br.* 24			
		1	4	62	58	36	*gr.* 40 *in.* 39 *br.* 1	— — —	*gr.* 13 *in.* 17 *br.* 13			
		1	3	60	11	52	*gr.* 35 *in.* 7 *br.* 15	— — *br.* 3	*gr.* 10 *in.* 3 *br.* 20			

No. of expt.	Parentage.	Number of seed parents.	Number of flowers.	Colour of resulting seeds.			Number of offspring.			Colour of corolla in offspring.		
				Green.	Inter.	Brown.	Hoary.	Inter.	Glabrous.	Hoary.	Inter.	Glabrous.
		1	4	58			*gr.* 30	—	*gr.* 10			
					30		*in.* 15	—	*in.* 11			
						46	*br.* 11	—	*br.* 24			
		1	3	48			*gr.* 21	—	*gr.* 22			
					41		*in.* 23	—	*in.* 13			
						38	*br.* 5	—	*br.* 32			
		1	2	21			*gr.* 12	—	*gr.* 4			
					—		—	—	—			
						47	*br.* 14	—	*br.* 17			
		1	?	225			*gr.* 121	—	*gr.* 39			
					112		*in.* 76	—	*in.* 16			
						241	*br.* 60	*br.* 22	*br.* 87			
		10	32 + ?	695	461	644	801	40	533			

c. *Subsequent Posterity derived from the foregoing* (*Table VI*).

In Experiments 52 and 53 (Table VI) we have results similar to those given in Table IV, the ratio of D to R being again not far from 1 : 1.

In Experiment 54, as in the comparable case in the preceding generation (Table V), we find that the number of glabrous plants is far too high; but that when the more hoary form 3*b* is substituted for the less hoary form 2 (Experiment 55), the result is exact—3D : 1R.

In Experiment 56, in which we should expect either 3D : 1R or else only dominants, according as the individual happened to be a DR or a pure D, it appears that three of the five individuals selected at random were DR and the remaining two pure D. Some of the offspring of the two latter plants, however, and also of one of the former, were half-hoary like the original hoary parent (type 2), or were even less hoary still, so that when quite young they might easily be mistaken for glabrous plants. Among the offspring of all the DR individuals there was the usual high percentage of recessives. In Experiment 57, a plant approaching the half-hoary character of type 2 (raised from (2 × 6) × self in Experiment 51) gave on self-fertilisation no offspring fully hoary, but only intermediate and glabrous plants.

Lastly, in the five remaining trials (Experiment 58), in which the seed parents were of recessive form, we have the expected proof of the purity of such recessives; for whether self-fertilised or crossed with a pure recessive, they invariably yielded recessives only.

To sum up the results in the two generations, we may conclude that Mendel's law holds for all the above cases except those in which a hoary cross-bred *originally derived from the half-hoary form* (2) is self-fertilised. In such cases the glabrous offspring are constantly in excess of the theoretical proportion of 1 : 3, while the hoary offspring often include many plants which exhibit various intermediate degrees of hoariness.

B. *Offspring of Cross-breds* (*D* × *R*) *when D and R were both brown-seeded.*

a. *When the Cross-breds were Fertilised with a Recessive Form.*

The results of the various experiments recorded in Table VII are strikingly different among themselves and altogether unexpected.

In Experiment 59, although the three pure forms 2, 5*c*, 5*a*, and the cross-bred parent (2 × 5*c*) were all brown seeded, yet the fruits resulting from the cross (2 × 5*c*) × 5*a* contained seeds of at least *two* colours—brown and green.

The colours were well-marked, less than 1 per cent. being classed as intermediates. With two or three exceptions the numbers in individual fruits (and naturally therefore in individual plants) showed a rough equality.

Table VI.—Experiments 52—58.

Number of experiment.	Parentage.	Number of seed parents.	Number of flowers.	Number of offspring.			Expected result.
				Hoary.	Inter.	Glabrous.	
	[(D × R_1) × R_2] × R_2. Seed parent hoary.						
52	[(2 × 6*a*) × (6*c* × self)] × [(6*c* × self) × self]	7	12	262	—	231	1D : 1R.
53	[(3*b* × 6*b*) × (6*c* × self)] × [(6*c* × self) × self]	2	3	36	—	42	,,
	[(D × R_1) × R_2] × self. Seed parent hoary.						
54	[(2 × 6*a*) × (6*c* × self)] × self	7	34	312	8	162	3D : 1R.
55	[(3*b* × 6*b*) × (6*c* × self)] × self	2	8	82	—	28	,,
	[(D × R_1) × self] × self. Seed parent hoary.						
56*a*	[(2 × 6*a*) × self] × self	3	3	33	—	14	3D : 1R, or all D, according as [(D × R_1) × self] was DR or D.
			5	68	—	29	
			4	90	7	53	
56*b*		2	4	88	32	—	
			6	—	78	—	
	[(D × R_1) × self] × self. Seed parent intermediate.						
57	[(2 × 6*a*) × self] × self	2	5	—	17	58	No definite prediction as to the result of this fertilisation was possible, since the plant used was neither half hoary like the one original parent, nor glabrous like the other, but intermediate between the two.
	[(D × R_1) × R_2] × R_2. Seed parent glabrous.						
58*a*	[(2 × 6*a*) × (6*c* × self)] × [(6*c* × self) × self]	11	?	—	—	583	All R.
58*b*	[(3*b* × 6*b*) × (6*c* × self)] × [(6*c* × self) × self]	2	2	—	—	56	,,
	[(D × R_1) × R_2] × self. Seed parent glabrous.						
58*c*	[(2 × 6*a*) × (6*c* × self)] × self	11	44	—	—	537	,,
58*d*	[(3*b* × 5*c*) × (5*a* × self)] × self	2	6	—	—	9	,,
	[(D × R_1) × self] × self. Seed parent glabrous.	3	8	—	—	56	,,
58*e*	[(2 × 6*a*) × self] × self						

Table VII.—Offspring obtained from Fertilising the Crossbreds (D × R) with a Recessive Form, when D and R were both brown-seeded.

No. of expt.	Parentage.	No. of seed parents.	No. of flowers.	Colour of resulting seeds.			Number of offspring.			Colour of corolla in offspring.		
				Green.	Inter.	Brown.	Hoary.	Inter.	Glabrous.	Hoary.	Inter.	Glabrous.
59	(2 × 5*c*) × (5*a* × self) (½ *H.wh.br.* × *G.r.br.*) × *G.wh.br.*	1	1	13		9						
			1	21		17						
			1	5		8						
		1	2	30		35						
			1	7	6	22						
		1	2	33		44						
		1	1	17		16						
			1	11		16						
			1	15	2	15						
		1	2	42		50						
			1	24		19	23	—	—	Purple.		
							—	—	19			White.

			3	42			41	—	—			
						42	—	—	41			
			2	40			39	—	—			
		1				44	—	—	42			
			1	9								
						10						
			1	16			16	—	—	Purple.		
						34	—	—	30			White.
			1	15								
						15						
		1	1	18								
						18						
			1	19								
						23						
		1	2	29								
						34						
	Total.........	8	26	406	8	471	119	—	132			
60	(2 × 5*c*) × (5*b* × self)	1	4	not	classified		121	—	2			
	(½*H.wh.br.* × *G.r.br.*) × *G.cr.br.*	1	2	,,	,,		33	1	2	Red and bluish-pink	White	Pinkish.
		1	5	,,	,,		94	3	11			
	Total.........	3	11				248	4	15			
61	(3*a* × 5*c*) × (5*a* × self)	1	1	41	—	—						
	(*H.wh.br.* × *G.r.br.*) × *G.cr.br.*	1	1	30	—	—	25	—	—			
		1	1	40	—	—	35	—	—			
			5	133	—	—	17	—	—	Purple.		
		.		(20 sown)								
					2		2	—	—			
						2	—	—	1			Red.
	Total.........	3	8	244	2	2	79	—	1			

Table VII—*continued.*

No. of expt.	rentage.	No. of seed parents.	No. of flowers.	Colour of resulting seeds.			Number of offspring.			Colour of corolla in offspring.		
				Green.	Inter.	Brown.	Hoary.	Inter.	Glabrous.	Hoary.	Inter.	Glabrous.
62	(3*a* × 5*c*) × (5*b* × self)	1	3	30			28	—	—	Purple (various).		
	(*H.wh br.* × *G.r.br.*) × *G.cr.br.*				2		2	—	—			
						53	52	—	—	Red, except 1 pink.		
		1	2	23			22	—	—			
						46	40	—	—			
		1	1	16 (10 sown)			10	—	—	Purple.		
						18 (10 sown)	9	—	—	Red, pink, and bluish-pink.		
	Total	3	6	69	2	117	163	—	—			
63	(3*b* × 5*c*) × (5*a* × self)	1	1	27	—	—	23	—	—	Purple.		
	(*H.wh.br.* × *G.r.br.*) × *G.wh.br.*		1	7 (5 sown)			5	—	—	Purple.		
		1				13 (5 sown)	3	—	2	Red, pink, and white		White.
			1	27			27	—	—			
						1	1	—	—			
				11			11	—	—			
		1	1		43		25	—	—			
						8	4	—	3			

		1	2	53	—	—	51	—	—			
		1	1	34			5	—	—			
					5		3	—	2			
						3	1	—	2			
	Total........	5	7	159	48	25	159	—	9			
64	(3*b* × 5*c*) × (5*b* × self) (*H.wh br.* × *G.r.br.*) × *G.cr.br.*	1	1	—	—	4	3	—	—	Red and pink.		
65	(2 × 5*c*) × (6*c* × self) (½*H.wh.br.* × *G.r.br.*) × *G.cl.gr.*	1	1	21			13	—	7			
						18	4	—	13			
		1	1	15			8	—	7			
						18	9	—	9			
	Total	2	2	36	—	36	34	—	36			

Sample sowings* (in each case of more than 100 seeds) further showed that the green seeds gave rise to hoary plants bearing purple flowers, a colour not found in either parents or grandparents, and the brown seeds to glabrous plants with white flowers like those of their recessive parent, and dominant grandparent. We may therefore conclude that the rough equality in the totals for seed-colour indicates in this case a corresponding agreement in the totals for the two kinds of plants differentiated as to flower-colour, and fair consistency with Mendel's ratio. There are indications that such correlation between the flower-colour and the leaf-character may sometimes, as here, be definite, though the experiments show considerable irregularities in this respect. (The 8 intermediates were not sown.)

In Experiment 60 in which (5*b*) was employed in place of (5*a*), the seeds though varying from brown to greenish were mostly of a nondescript intermediate tint difficult to classify. As the seeds could not be satisfactorily sorted all were sown, *and* 252 *hoary* (*including* 5 *intermediates*) *and only* 15 *glabrous plants* were obtained instead of 3 : 1. The latter plants bore pink flowers. Of the former some fifteen specimens were grown to maturity, and bore flowers varying from red to bluish-pink. Coincident with the absence of typical green seeds, we have the complete disappearance of the purple flowers characteristic of the corresponding offspring in the preceding experiment, and the occurrence of the red or pink shades frequently observed after a cross with 5*c* (red) or with the cream-coloured form 5*b*. The intermediates bore white flowers like their intermediate grandparent.

Results somewhat similar as regards the character of the offspring, and equally at variance with the expected ratio, were obtained from two other unions (Experiments 61 and 63). In both these cases only a very small proportion of the offspring were glabrous (79D 1R and 159D 9R). Of these the one in Experiment 61 resembled its more remote recessive progenitor R_1 in flower-colour (red); the two which flowered in Experiment 63 were white like their recessive parent R_2, and also their dominant grandparent.

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* When the seeds were sorted, those obviously bad were discarded; the numbers given in the tables therefore only include such as appeared likely to germinate.

When the seeds were of mixed colours, a sample sowing of those which presented some definite colour sometimes sufficed to indicate the character (whether hoary or glabrous) of the whole class. If a uniform result was obtained the remainder of the same class were not sown.

But in regard to other seed-colour categories, want of uniformity of tint, or the occurrence of a mixed result as regards leaf character, made a full sowing necessary. In such cases the calculated totals of hoary and glabrous plants are based upon the *total* numbers of each seed-colour irrespective of the *particular* number of any colour which failed to germinate. The assumption that equal proportions of the differently coloured seeds would have failed to germinate may, however, introduce an appreciable error.

In Experiment 64 the offspring were too few (three) to give a decisive result.

In Experiment 62 the disappearance of the recessive form appears to be complete; *for we have the remarkable result that out of a total offspring numbering* 163, *not a single plant was glabrous*, though two of these seed-plants gave mixed offspring on self-fertilisation in Experiment 67. Finally, in Experiment 65, in which R_2 differs in seed-colour from R_1, we have a Mendelian result, both as regards seed-colour and leaf-character. These results will be considered in connection with the general statement of conclusions.

In regard to seed-colour the results were no less puzzling. In all cases the seeds were mixed. In the two experiments (59 and 65) in which a nearly Mendelian result was obtained, we find complete correlation between seed-colour and leaf-character in the former, and distinct evidence to the contrary in the latter. In Experiment 63 the correlation is imperfect; green seeds produced hoary plants, but brown seeds produced both forms. In Experiment 61 there is also some indication of correlation. In Experiment 62, on the other hand, the seed-colours afforded no clue, for all alike gave rise to hoary plants.

These results will be discussed hereafter. Attention must be directed to the fact that while on the one hand unions in the form $DR_1 \times R_2$ gave Mendelian results in both trials in which R_1 and R_2 were green-seeded, and in the one trial in which R_1 was brown-seeded and R_2 green-seeded; those in which R_1 and R_2 were both brown-seeded did so in one case only out of five. It is characteristic of these aberrant cases that there is an overwhelming preponderance of dominants. This discrepancy is certainly not fortuitous; *for either the one or the other result can be obtained from the same DR individual by an appropriate selection of the second recessive parent.* (See Experiments 85 and 87.)

What determines the several results is entirely unknown. R_1 differs from R_2, so far as we can tell, in nothing but colour.

b. When the Cross-breds were Self-fertilised.

Turning now to the results obtained on self-fertilisation (Table VIII), in Experiment 66, as in the previous case in which the half-hoary form (2) was used (Experiment 51), the glabrous offspring were far in excess of the Mendelian proportions of 1 : 3. Allowing for the possibility that seedlings which "damped off" very early, classified as glabrous, may, in reality, have been intermediates, the excess would remain considerable. The flowers of the glabrous offspring were white or pink, not red as in the recessive parent; those of the hoary plants white, pink, or red. The seeds were not classified.

In Experiment 67 there is a similar discrepancy between the expected and the observed results, 245D 131R instead of 3 : 1, although in this case the dominant parent (3*a*) was a fully hoary

Table VIII.—Offspring obtained from the Self-fertilisation of the Cross-breds (D × R) when D and R were both brown-seeded.

No. of expt.	Parentage.	Number of seed parents.	Number of flowers.	Colour of resulting seeds.			Number of offspring.			Colour of corolla in offspring.	
				Green.	Inter.	Brown.	Hoary.	Inter.	Glabrous.	Hoary.	Glabrous.
66	(2 × 5*c*) × self	1	4	Not classified			62	12	35	Red, white, and bluish-pink	Pink, white, and pinkish-white.
	(½ *H. wh. br.* × *G. r. br.*)	1	6	,,	,,		61	5	42		
		1	2	,,	,,		42	2	22		
		1	5	,,	,,		50	6	40		
		1	3	,,	,,		63	5	35		
		1	1	,,	,,		14	5	1		
		1	3	,,	,,		80	16	44		
		1	1	,,	,,		16	1	19		
	Total	8	25				388	52	238		
67	(3*a* × 5*c*) × self	1	1	6			5	—	1	Purple (various) Pink, white, and bluish-pink	Purple (various). Pink.
	(*H. wh. br.* × *G. r. br.*)					24	15	—	9		
		1	1	10			8	—	2		
						25	17	—	8		
		1	?	110			51	—	34		
					121		53	—	30		
						15	7	—	7		
		1	?	63			43	—	15		
					63		42	—	20		
						11	4	—	5		
	Total ..	4	2 + ?	189	184	75	245	—	131		

No. of expt.	Parentage.	Number of seed parents.	Number of flowers.	Colour of resulting seeds.			Number of offspring.			Colour of corolla in offspring.	
				Green.	Inter.	Brown.	Hoary.	Inter.	Glabrous.	Hoary.	Glabrous.
68	(3*b* × 5*c*) × self (*H. wh. br.* × *G. r. br.*)	1	2	—	—	All	49	—	11		
		1	1	—	—	,,	30	—	9		
		1	1	—	—	,,	21	—	8		
		1	?	—	—	,,	31	—	9		
		1	?	—	—	,,	221	—	81		
	Total	5	4 + ?	—	—	All	352	—	118		

form. The flowers of plants, whether glabrous or hoary, derived from green seeds, were purple; those from brown seeds, pink or more rarely white; on the other hand, there appeared to be *no* correlation between *seed-colour* and *leaf-character* in this particular case.

In Experiment 68 we have the exact result 3D : 1R. The seeds, unlike those in the two preceding experiments, were all of one colour, brown. The plants were destroyed before flowering.

The results in Experiments 66 and 68 confirmed those obtained in Experiments 51, 54, 55. The cross-breds *3b* × a recessive (whether green- or brown-seeded) gave a Mendelian result on self-fertilisation; whereas hybrids arising from the half-hoary type 2 × a recessive gave, on self-fertilisation, more than half the total offspring recessive. In Experiment 67—the case of cross-breds *3a* × *5c*—though *3a* is a form to all appearances similar to *3b*, the result of self-fertilisation is of the same exceptional character as that given by the cross-breds containing the half-hoary type.

c. *Subsequent Posterity derived from the foregoing.*

In Experiments 69—74 we have results obtained from a third crossing with a recessive form, when R_2 was again used as the recessive parent $(DR_1 \times R_2) \times R_2$. All the individual matings in four combinations, and seven out of eight matings in the fifth combination (Experiment 73), gave results in good agreement with the expected 1D : 1R. The exceptional individual in the fifth combination gave all (twenty-one) dominants. This individual had red flowers, whereas the other seven plants were various shades of purple. In the remaining combination, however (Experiment 72), the numbers obtained showed a ratio of 2D : 1R; nor could the total result be traced (as in Experiment 73) to the exceptional behaviour of individuals. From each fruit, as well as from each plant, the result was the same—a distinct majority of the hoary form.

Experiments 75—77 give the corresponding results when each successive cross was made with a recessive parent of a different flower-colour $(DR_1 \times R_2) \times R_3$. Here the offspring were almost all of the dominant form, only a single individual giving the expected result 1D : 1R. From the rest taken together, three recessives alone were obtained out of a total offspring of 397. Now two of the three seed parents which gave the result in Experiment 77 gave a Mendelian result in Experiment 73, and three out of the eight plants used in Experiment 75 were among those used in Experiment 72; moreover, the same pollen parents were used in Experiments 69, 71, 73 as in Experiments 75 and 76; and again in Experiments 70 and 74 as in Experiments 72 and 77.

Table IX.—Offspring obtained from [(D × R_1) × R_2].

a. When the seed parent is hoary and is crossed with R_2.
b. ,, ,, ,, ,, ,, ,, R_3.
c. ,, ,, ,, glabrous ,, ,, R_2 or R_3.
d. ,, ,, ,, hoary ,, self-fertilised.

Number of experiment.	Parentage.	Number of seed plants.	Number of flowers.	Number of offspring.		Expected result.
				Hoary.	Glabrous.	
	a.					
69	[(2 × 5*c*) × (5*a* × self)] × [(5*a* × self) × self]	4	9	97	106	1D : 1R.
70	[(2 × 5*c*) × (5*b* × self)] × [(5*b* × self) × self]	4	8	138	138	,,
71	[(3*a* × 5*c*) × (5*a* × self)] × [(5*a* × self) × self]	3	8	77	94	,,
72	[(3*a* × 5*c*) × (5*b* × self)] × [(5*b* × self) × self]	5	7	114	57	,,
73*a*	[(3*b* × 5*c*) × (5*a* × self)] × [(5*a* × self) × self]	7 (purple flowered)	10	133	131	,,
73*b*		1 (red flowered)	2	21	—	,,
74	[(3*b* × 5*c*) × (5*b* × self)] × [(5*b* × self) × self]	1	1	19	21	,,
	b.					
75	[(3*a* × 5*c*) × (5*b* × self)] × [(5*a* × self) × self]	8	10	335	2	,,
76*a*	[(3*b* × 5*c*) × (5*b* × self)] × [(5*a* × self) × self]	1	2	27	—	,,
76*b*		1	1	24	23	,,
77	[(3*b* × 5*c*) × (5*a* × self)] × [(5*b* × self) × self]	3	3	32	1	,,
	c.					
78	[(2 × 5*c*) ×.(5*b* × self)] × [(5*b* × self) × self]	3	6	—	163	All R.
79	[(3*b* × 5*c*) × (5*a* × self)] × [(5*a* × self) × self]	2	3	77	1	,,
80	[(3*b* × 5*c*) × (5*a* × self)] × [(5*b* × self) × self]	1	1	17	—	,,
	d.					
81	[(3*a* × 5*c*) × (5*a* × self)] × self	2	10	140	89	3D : 1R, or all D, according as [(D × R_1) × R_2] was DR or D.
82	[(3*a* × 5*c*) × (5*b* × self)] × self	7	30	250	118	
83	[(3*b* × 5*c*) × (5*a* × self)] × self	3	several	146	65	
84	[(3*b* × 5*c*) × (5*b* × self)] × self	2	9	119	41	

Otherwise expressed:—

Individuals used as ♀s	in Experiment 73 gave a Mendelian result when crossed with R_2. in Experiment 77 gave an aberrant result when crossed with R_3.

also

Individual recessives used as ♂s in the third pollination	in Experiments 69, 71, 73 gave a Mendelian result. in Experiments 75 and 76 gave an aberrant result. also in Experiments 70 and 74 gave a Mendelian result. in Experiment 77 gave an aberrant result.

Therefore the difference between the results can scarcely be attributed merely to the individual constitutions of either parent, but must be due to some relation subsisting between the two.

The fewness of recessives occurring among the offspring in the $(DR_1 \times R_2) \times R_3$ unions as compared with those obtained from the $(DR_1 \times R_2) \times R_2$ unions, recalls the results obtained in the second generation, where the same DR cross-bred plant was found to give varying proportions of recessive offspring according to the particular R form with which it was next crossed, and confirms the observation then made, that *the order in which the recessive forms are used* seems to have an effect in determining the proportion of hoary and glabrous offspring. The fact nevertheless remains, that the only visible difference between the successive glabrous pollen parents was in colour.

In regard to the seed-colours, which are omitted from the accompanying table (Table IX), there was sometimes diversity, sometimes uniformity, but in any given union, either the one condition or the other usually prevailed in all matings.

The seed-colour was sometimes correlated with the leaf-character and sometimes not. When correlation occurred, brown seeds produced glabrous plants, and green seeds hoary plants; the intermediates were too few to allow of any generalisation.

Such correlation was observed in Experiments 69 and 71, with the exception of four seeds (which possibly were wrongly classified); in Experiment 73 (another repeated cross with the white-flowered 5*a*) in six out of the seven matings giving the Mendelian result; also probably in Experiments 75 and 77 (an alternate cross with white- and cream-flowered recessives). In Experiments 70, 72, and 74 (a repeated cross with a cream-flowered recessive), and in Experiment 76, the seeds were not easily classified in regard to colour.

As regards Experiments 78—80, where the final seed parent was glabrous, we have a normal Mendelian case in 78, the offspring being all glabrous. But in 79 and 80 the result is puzzling and entirely inexplicable upon the Mendelian theory, for these two unions between plants of the recessive form gave offspring which, with a solitary exception, *were all dominants.* It may be added that the two final seed parents from which this unexpected result was obtained were sister plants to the exceptional individual previously mentioned in Experiment 73 as having given *all dominants* when crossed with a recessive. (See Conclusions, p. 86.)

The three exceptional plants arose from a cross between a cross-bred and an individual pure recessive (5*a*) which was used as pollen parent in several parallel experiments giving normal results. That cross gave both green and brown seeds, the three exceptional plants (one hoary and two glabrous) all arising from the latter. Sister plants arising from the green seeds were all hoary, and three of them contributed to the Mendelian result in Experiment 73.

Fortunately the two exceptional glabrous plants were also self-fertilised, and the result in this case was precisely the same as in all other cases of self-fertilisation of individuals of the recessive form—the offspring were all glabrous (see p. 79). But for this result one might have been tempted to suppose that some error had occurred in recording the leaf-character in these two plants. It seems equally improbable that in the final cross any such mistake as the unintentional taking of pollen from a hoary individual similar in colour to the recorded glabrous parent can have been made. Such an explanation would still leave the result in Experiment 80 unexplained, since at the time that this experiment was made, no *cream*-flowered *hoary* plants had ever been seen. These two cases, then, remain as the solitary instances among all the various unions that were made, of the occurrence of *dominant* offspring when both parents belong to a *recessive* type.

The results of Experiments 81—84, in which hoary cross-breds of the form ($DR_1 \times R_2$) were self-fertilised, are on the whole confirmatory of those obtained from the self-fertilisation of the (DR_1) cross-breds from which they were derived. In the two cases in which the dominant ancestor was the hoary form 3*a* (Experiments 81, 82), the proportion of recessive offspring obtained from the ($DR_1 \times R_2$) cross-breds was, as in the case of the (DR_1) cross-breds, considerably in excess of the theoretical result 3D : 1R. When 3*b* was employed as the dominant parent in place of 3*a* (Experiments 83, 84), we get a Mendelian result (3D : 1R) from two cross-breds of the form [(3*b* × 5*c*) × 5*b*], as we did from their cross-bred ancestors (3*b* × 5*c*). On the other hand, from two of the three cross-breds of the form $[(3b \times 5c) \times 5a]$, which contributed to the total result 146D 65R (in Experiment 84), the proportion of recessives is a good deal too high.

2. *Offspring of Cross-breds produced from* ($R \times D$).

a. *When the Cross-breds were Fertilised with a Recessive Form* (*Table X*).

a. In Experiment 85, in which the cross-breds ($5a \times 1$) were crossed with a recessive of the same type as the recessive parent $5a$, every fruit contained green and brown seeds in very varying proportions, and usually a few intermediates. All the intermediates (16) were sown, and glabrous plants only were obtained from them; samples of green and brown seeds gave all hoary (33) and all glabrous (16) plants respectively. Correlation between leaf-surface and seed-colour was apparently complete. On the assumption that all the green seeds would have produced hoary plants, and all those not green, glabrous plants, the offspring from every fruit would have been mixed, and the total numbers would have been in the proportion 228 hoary and 191 glabrous, as compared with the expected result 1D : 1R.

In Experiment 86, in which the cross-breds ($5b \times 1$) were crossed with a recessive of the same type as the recessive parent $5b$, every fruit contained seeds of the three colours. None of the colours were strictly correlated with either leaf-character, hoary plants being obtained from almost all the green, most of the intermediate, and some of the brown seeds. It was therefore necessary to make full sowings, in order to ascertain the relative numbers of the two leaf-characters: 297 hoary and 302 glabrous plants were obtained.

In both these experiments, 85 and 86, the recessive forms successively employed were alike in flower-colour, and in both it will be noticed that the results are in agreement with Mendel's ratio.

In the four following experiments (87—90), in which R_1 and R_2 were of different flower-colour, and both brown in seed-colour, we see the same more or less complete disappearance of the glabrous form which has already been noted in Experiments 60, 63, 75, 77, although some of the seed parents employed, *e.g.*, in Experiment 87, were the same as those which gave normal results in Experiment 85. In two cases (Experiments 87, 88) in which the seeds were of mixed colours, there was some degree of correlation between seed-colour and leaf-character, the few glabrous plants that were obtained being all derived from brown and intermediate seeds. In a third case (Experiment 90) no such correlation occurred; green, brown, and intermediate seeds alike yielded hoary plants only. In the remaining case (Experiment 89) in which the seeds were all green, the offspring obtained from a sample sowing were again exclusively hoary.

In Experiment 91, in which R_1 and R_2, unlike in flower-colour, were both *green* in seed-colour, green and intermediate coloured seeds were produced, but not brown. Both occurred in every fruit, and both gave rise to hoary and glabrous plants, the totals in the case of both seeds and plants being fairly consistent with Mendel's ratio (82 green, 70 intermediate : 64 hoary, 76 glabrous).

These remarkable results are in harmony with those obtained from the (D × R) cross-breds (Table VI), and show that when the same recessive strain is introduced in each successive cross, Mendel's law holds; but that the successive use of recessive strains of different colour may exert some disturbing effect upon the numerical relation of the two kinds of offspring—an effect of which the data at present to hand afford no explanation. (See Conclusions, p. 86.)

b. *Offspring obtained when the Cross-breds were Self-fertilised.*

In Experiment 92 (Table XI) the cross-breds ($5a \times 1$), of which several were among the number of those previously used for Experiments 85, 87, were self-fertilised. Every cross-bred produced green, brown, and intermediate seeds, the proportion of green to non-green being roughly 3 : 1, except in one mating, in which only one fruit was gathered. Sample sowings showed complete correlation between seed-colour and leaf-characrer, green seeds giving rise to hoary, brown and intermediate to glabrous plants. Presumably, therefore, the total number of plants would have been in the proportion 1244 hoary and 407 glabrous—a very close approximation to the Mendelian ratio 3 : 1.

In Experiment 93 cross-breds ($5b \times 1$), several of which had been previously used for Experiments 86 and 88, were self-fertilised. The resulting seeds were mixed, but in very varying proportions. The number of intermediates was large—nearly one-fourth of the total number. Of the samples sown, green seeds again produced hoary plants; brown seeds, with four exceptions, glabrous plants, unless these four seeds should more properly have been included among the intermediates. The intermediates, however, yielded both forms, and it was therefore necessary to sow the whole number. Unfortunately, a large proportion—more than 100—failed to germinate. If, however, we may suppose that no considerable error is due to this fact, then, assuming perfect correlation in the case of the two other colours (four seeds excepted), the total number of plants would have been in the proportion 1429 hoary, 373 glabrous, or as 3·8 : 1.

In each of the three following experiments (94—96) only a single cross-bred was self-fertilised. The seeds were difficult to sort, and a full sowing was therefore necessary. In the case of the cross-bred ($5d \times 1$) (Experiment 94), an exact Mendelian result was obtained (117D, 39R). With the cross-breds ($5e \times 1$) and ($6c \times 1$), however, the numbers showed a considerable deviation from the expected result—98 D to 18 R in the former case, 175D to 39R in the latter.

TABLE X.—Offspring obtained from Fertilising the Cross-breds (R × D) with a Recessive Form.

No. of expt.	Parentage.	No. of seed parents.	No. of flowers.	Colour of resulting seeds.			No. of offspring.		Colour of corolla in offspring.	
				Green.	Inter.	Brown.	Hoary.	Glabrous.	Hoary.	Glabrous.
85	(5*a* × 1) × (5*a* × self) (*G.wh.br.* × *H.wh.bl.*) × *G.wh.br.*	1	2	60	3	43	*gr.* 21 — —	— *in.* 3 *br.* 11	Purple.	White.
		1	1	25 (12 sown)	1	12 (5 sown)	*gr.* 12 — —	— *in.* 1 *br.* 5		
		1	1	30	5	29	— — —	— *in.* 5 —		
		1	1	38	2	21	— — —	— *in.* 2 —		
		1	1	39	2	18	— — —	— *in.* 2 —		
		1	1	19	—	43	— — —	— — —		
		1	1	17	3	9	— — —	— *in.* 3 —		
	Total............	7	8	228	16	175	33	32		

	(G.cr.br. × H.wh.bl.) × G.cr.br.				31	42				
		1	5	51			gr. 5	gr. 3		
					82		in. 14	—	Purple, red	Cream, white.
						51	br. 12	br. 22		
		1	3	77			gr. 37	—	Red	Cream, white.
					51		in. 27	in. 15		
						76	br. 10	br. 65		
		1	2	41			gr. 8	—		
					34		in. 28	in. 5		
						59	—	br. 53		
		1	2	48			gr. 39	—		
					39		in. 21	in. 4		
						65	br. 28	br. 52		
		1	2	49			gr. 25	—		
					46		in. 31	in. 9	Purple.	
						44	br. 1	br. 43		
		1	1	19			gr. 19	—		Cream, white.
					15		in. 12	in. 3	Purple.	
						29	—	br. 28		
										Cream, white.
	Total............	7	18	360	298	366	297	302		
87	(5a × 1) × (5b × self)	1	2	97	—	—				
		1	1	58	—	—	gr. 40	—		
	(G.wh.br. × H.wh.bl.) × G.cr.br.	1	1	56	—	—	gr. 47	—		
		1	1	57 (12 sown)			gr. 11	—	Purple.	
					1		—	in. 1		
						6	—	br. 1		White.
										White.
	Total...	4	5	268	1	6	98	2		
88	(5b × 1) × (5a × self)	9	13	∞ (98 sown)			gr. 73	—	Purple (various).	
	(G.cr.br. × H.wh.bl.) × G.wh.br.				7		in. 5	in. 1		
						2	—	br. 2		
										White.
	Total............	9	13	∞	7	2	78	3		

Table X—*continued.*

No. of expt.	Parentage.	No. of seed parents.	No. of flowers.	Colour of resulting seeds.			No. of offspring.		Colour of corolla in offspring.	
				Green.	Inter.	Brown.	Hoary.	Glabrous.	Hoary.	Glabrous.
89	(5*c* × 1) × (5*a* × self) (*G.r.br.* × *H.wh.bl.*) × *G.wh.br.*	1	2	101 (24 sown)	—	—	23	—	Purple.	
90	(5*d* × 1) × 5*b* × self) (*G.pk.wh.br.* × *H.wh.bl.*) × *G.cr.br.*	1	1	12	19	17	*gr.* 1 *in.* 11 *br.* 17	— — —		
		1	3	60	22	85	*gr.* 14 *in.* 18 *br.* 21	— — —		
	Total	2	4	72	41	102	82	—		
91	(6*d* × 3*a*) × (6*c* × self) (*G.li.gr.* × *H.wh.br.*) × *G.cl.gr.*	1	2	43	24		*gr.* 21 *in.* 9	*gr.* 17 *in.* 15	Purple (various) White, pinkish-white	Purple (various). White, pinkish-white.
		1	1	12	9		*gr.* 4 *in.* 2	*gr.* 8 *in.* 7		
		1	1	18	22		*gr.* 10 *in.* 9	*gr.* 4 *in.* 12		
		1	1	9	15		*gr.* 3 *in.* 6	*gr.* 5 *in.* 8		
	Total	4	5	82	70	—	64	76		

Table XI.—Offspring obtained from the Self-fertilisation of hoary Cross-breds (R × D).

No. of expt.	Parentage.	No. of seed parents.	No. of flowers.	Colour of resulting seeds.			No. of offspring.		Colour of corolla in offspring.	
				Green.	Inter.	Brown.	Hoary.	Glabrous.	Hoary.	Glabrous.
92	(5*a* × 1) × self (*G.wh.br.* × *H.wh.bl.*)	1	6	270	26	57	—	*in.* 16		
		1	3	152	3	41	—	*in.* 3		
		1	1	58	2	5	—	*in.* 1		
		1	1	47	3	11	—	*in.* 1		
		1	3	139	9	32	—	*in.* 5		
		1	5	229	15	71	—	*in.* 11		
		1	4	177	12	54				
		1	4	172 (59 sown)	6	60 (32 sown)	*gr.* 59 — —	— *in.* 5 *br.* 32	Purple.	White.
	Total........	8	27	1244	76	331	59	74		

Table XI—*continued.*

No. of expt.	Parentage.	No. of seed parents.	No. of flowers.	Colour of resulting seeds.			No. of offspring.		Colour of corolla in offspring.	
				Green.	Inter.	Brown.	Hoary.	Glabrous.	Hoary.	Glabrous.
93	(5*b* × 1) × self (*G.cr.br.* × *H.wh.bl.*)	1	1	35 (12 sown)	13	16	*gr.* 12 *in.* 8 *br.* 1	— *in.* 2 *br.* 10	Purple.	Cream, white.
			?	153 (12 sown)	46	54 (12 sown)	*gr.* 10 *in.* 25 —	— *in.* 1 *br.* 11	Purple.	Cream, white.
		1	1	43 (12 sown)	25	—	*gr.* 10 *in.* 12 —	— *in.* 7 —	Purple, except 1 pink.	White.
		1	?	134 (12 sown)	44	65 (12 sown)	*gr.* 12 *in.* 29 —	— — *br.* 11	Purple.	White.
			1	40	23	9	*in.* 15 —	*in.* 6 *br.* 9		
		1	1	34	20	11	*in.* 14 —	*in.* 2 *br.* 10		
		1	1	56	13	8	*in.* 11	—		

		1	1	47	19	7	*in.* 13	*in.* 4		
		1	1	38	20	11	*in.* 17 *br.* 1	— *br.* 10		
		1	4	168	86	30	*in.* 44	*in.* 8		
		1	1	37	14	14	*in.* 10 —	*in.* 5 *br.* 14		
		1	2	72	30	24	*in.* 26	—		
		1	1	47	5	17	*in.* 1 *br.* 2	— *br.* 7		
		1	1	34	27	16	*in.* 13	*in.* 3		
		1	2	77	28	21	*in.* 16	*in.* 2		
		1	1	34	19	18	*in.* 15	—		
	Total..........	14	19	1049	432	321	317	122		
94	(5*d* × 1) × self (*G.pk.wh.br.* × *H.wh.bl.*)	1	?		Not classified		117	39	Purple	White.
95	(5*e* × 1) × self (*G.bl.pk.br.* × *H.wh.bl.*)	1	?		,,	,,	98	18	Purple, white	Purple, white.

Table XI—*continued.*

No. of expt.	Parentage.	No. of seed parents.	No. of flowers.	Colour of resulting seeds.			No. of offspring.		Colour of corolla in offspring.	
				Green.	Inter.	Brown.	Hoary.	Glabrous.	Hoary.	Glabrous.
96	(6*c* × 1) × self (*G.cl.gr.* × *H.wh.bl.*)	1	?	Not classified.			175	39	Purple, white. pink	Purple, white, pink.
97	(6*c* × 3*a*) × self (*G.cl.gr.* × *H.wh.br.*)	1	1	32		8	*gr.* 20 *br.* 6	*gr.* 9 *br.* 2	Pink, bluish-pink White	Pink, bluish-pink. White.
		1	1	30		12	*gr.* 20 *br.* 7	*gr.* 10 *br.* 4		
	Total..........	2	2	62	—	20	53	25		

In Experiment 97, in which the cross-breds ($6c \times 3a$) were self-fertilised, green and brown seeds were obtained in the proportion of 3 to 1. There was no correlation between seed-colour and leaf-character, for each colour gave rise to both kinds of plants. The totals 53D and 25R show too high a proportion of the glabrous form, a result which entirely agrees with that obtained from the self-fertilisation of the other set of cross-breds in which the hoary type *3a* was used as the dominant parent (Experiment 67).

From (R × D) × self, therefore, close Mendelian results were obtained in three out of the five cases in which the D parent was of the hoary type 1, viz., in those in which the R parent had white, cream, or pinkish-white flowers; but when the R parent had bluish-pink or claret-coloured flowers, there was a deficiency of R offspring. On the other hand, when the type *3a* was used as the D parent, there was too high a proportion of R plants.

c. *Offspring of Dominant Cross-breds produced in* 2a (*Tables XII and XIII*).

In accordance with the Mendelian hypothesis, all dominant cross-breds resulting from the cross (R × D) × R, are of the class of impure dominants, and when self-fertilised, yield D and R in the proportion of 3 to 1. We should therefore expect all the final seed parents in Experiments 98—102 (Table XII) to yield a mixed offspring in which the proportion of hoary to glabrous is as 3 to 1. On the other hand, dominants resulting from (R × D) × self are by theory of *two* kinds—(1) impure dominants as above, and (2) pure dominants, which, when self-fertilised, yield dominants and dominants only. In Experiments 103—107 (Table XIII) we should therefore expect the results to vary, according as the final seed-parents selected at random belonged to the former or the latter class.

In Experiments 98 and 99, in which cross-breds of the form $[(R_1 \times D) \times R_1]$ were self-fertilised, there is close agreement between the observed and the theoretical result, 3D : 1R.

In Experiments 100—102 (Table XII), in which cross-breds of the form $[(R_1 \times D) \times R_2]$ were self-fertilised, we find that some of the cross-breds give the expected result 3D : 1R; others on the contrary yielded *only dominants*.

This fact is the more surprising since such cross-breds giving one a Mendelian and another an aberrant result, may be sister plants, derived by self-fertilisation from the same parent.

In Experiments 103—107, in which fourteen individuals selected at random from among the dominant offspring of various self-fertilised (R × D) cross-breds were self-fertilised, eight were evidently pure dominants, and produced only dominants, six were impure dominants,

Table XII.—Offspring obtained by Self-fertilisation of [(R × D) × R] when it is Hoary.

Number of experiment.	Parentage.	Number of seed parents.	Number of flowers.	Number of offspring.		Expected result.
				Hoary.	Glabrous.	
98	[(5*a* × 1) × (5*a* × self)] × self	2	18	298	95	3D : 1R.
99	[(5*b* × 1) × (5*b* × self)] × self	3	12	364	113	
100*a*	[(5*a* × 1) × (5*b* × self)] × self	1	?	105	—	
100*b*		1	?	73	29	
101	[(5*b* × 1) × (5*a* × self)] × self	3	24	348	110	
102*a*	[(6*d* × 3*a*) × (6*c* × self)] × self	1	5	94	—	
102*b*		2	5	68	17	

Table XIII.—Offspring obtained by Self-fertilisation of [(R × D) × self] when it is Hoary.

Number of experiment.	Parentage.	Number of seed parents.	Number of flowers.	Number of offspring.		Expected result.
				Hoary.	Glabrous.	
103*a*	[(5*a* × 1) × self] × self	4	12 or more	374	141	3D : 1R, or all D, according as [(R × D) × self] was DR or D.
103*b*		3	8 or more	372	—	
104	[(5*b* × 1) × self] × self	1	12	190	—	
105	[(5*d* × 1) × self] × self	1	2	101	—	
106*a*	[(5*e* × 1) × self] × self	2	2	12	3	
106*b*		1	1	48	—	
107*a*	[(6*c* × 1) × self] × self	1	4	63	14	
107*b*		1	8	70	—	

and yielded a mixed offspring, in one experiment 374D, 141R, in the second 12D, 3R, and in the third, 62D, 14R.

d. *When the Cross-breds were Fertilised with a Dominant Form.*

When some of the various (R × D) cross-breds used in the preceding experiments were crossed with the same hoary white-flowered Brompton Stocks, (*7a* and *7b*), used in the experiments described in Table II, the resulting offspring (148) were, in accordance with expectation, all hoary.

III. *Purity of "Extracted" Recessives and Dominants.*

According to the Mendelian hypothesis, such recessives are pure, and should behave as though they were of unmixed descent. If this be the case, they should, when self-fertilised, produce recessives and recessives only. To test this particular point, many such extracted recessives were self-fertilised, and thus produced more than 1000 offspring, all of which were recessive, so far confirming the anticipation as to their purity.

At the same time we have the contradictory result mentioned in Experiments 79 and 80, that from two such extracted recessives crossed with a *pure* recessive (the product of two generations of self-fertilisation), 94 *dominants were obtained and a single recessive.* This result is unexplained.

Purity of extracted *Dominants* was shown in Experiments 103*b*, 104, 105, 106*b*, 107*b*.

IV. *Nature of Recessives produced in the First Crosses.*

These first-cross recessives, when self-fertilised for two generations, invariably gave recessive offspring, having flower- and seed-colours identical with those of the original glabrous parent. The number thus produced, by several individuals, amounted to more than 200 in the first generation and about 130 in the second.

The question whether such recessives can have been the result of accidental self-fertilisation was considered (p. 44), and at present we strongly incline to think that they were not, while fully recognising the difficulties this view entails.

V. *Time of Flowering of Cross-breds.*

Of the original types, some were annual, some biennial.

Only a limited number of observations were made upon the inheritance of these qualities, owing to the difficulty of sowing and planting such large numbers simultaneously. The biennial forms (viz., *incana* (type 1), and the various Brompton strains), do not bloom in the first season, but in the second year they usually flower some weeks before the annuals. *With rare exceptions, all cross-bred plants and "extracted" types flowered in the first season.* The offspring of various crosses between annual forms flowered at the same time whether they were hoary or glabrous; but among the offspring of various crosses between hoary biennials and glabrous annuals it was usual for the recessives to flower before the dominants. In fact, the difference in time in some cases was sufficient for the former to be almost over before the latter had well begun. A certain number of these extracted recessives, however, flowered simultaneously with the dominants obtained from the same mating. Very rarely such recessives produced no flowers at all in the first year: in such cases the habit of growth of these plants resembled that of the biennial forms.

VI. *Summary of Conclusions from Experiments with Matthiola.*

The results obtained are so complex that it is difficult to draft statements which shall give a precise and comprehensive view of the phenomena.

Generally speaking, the following rules hold good:—

1. In crosses between hoary and glabrous plants, the former character was dominant, the latter recessive.

2. Such cross-breds, whether self-fertilised, or fertilised with a dominant, or with the original recessive parent, obeyed Mendel's law with fair consistency.

3. Dominant cross-breds, however, fertilised with a recessive *other than the original one*, gave results apparently of two kinds. Some gave the expected Mendelian equality while others gave *all or almost all dominants;* though several such individuals which gave this excess of dominants on fertilisation with a *new* recessive, produced the usual mixture on self-fertilisation. Two individuals, however (Experiments 100*a* and 102*a*), *produced no recessives at all on self-fertilisation* (see p. 77).

4. Similar results (as in 2 and 3), occurred when dominants produced by the second cross with recessives, were again fertilised with recessives.

5. Other notable exceptions to the rule that dominant cross-breds generally fulfil the Mendelian expectation, were seen when two particular types (2 and 3*a*) of hoary plants were used. Type 2 is the "half-hoary" form, but type 3*a* is a fully hoary form. Dominant cross-breds raised from these, when fertilised with *recessives*, gave a Mendelian result; but on self-fertilisation the proportion approaches 1·7D : 1R (calculated from Experiments 51, 66, 67, 97).

6. No plant showing the peculiar feature of the "half-hoary" Type 2 was ever produced as offspring of any of the crosses between the fully hoary and glabrous types, and, indeed, no plant intermediate between these two types ever occurred as the result of such unions.

7. Crosses between the half-hoary type and recessives gave in the first generation fully hoary cross-breds with only two half-hoary exceptions. Of the mixed offspring derived from these fully hoary cross-breds the great majority of dominants were again fully hoary; some, however, were half-hoary, and some intermediate between the half-hoary and the glabrous forms. No line could be drawn between such intermediates and the half-hoary plants, and therefore all are classed together as "intermediate" in the tables. It is possible that the fully hoary cross-breds are DR, and the others DD, but the numbers do not accord well with this simple explanation.

8. Crosses between white-flowered hoary and variously coloured glabrous forms commonly gave purple-flowered offspring (sometimes, however, a blend, *e.g.*, pink from red and white). This fact, and that given in 7, indicate that the first-cross offspring sometimes present atavistic characters. Crosses between different *coloured* pure types were for the most part not made (see p. 46).

9. The results of self-fertilising cross-breds produced by parents of dissimilar colour was usually to reproduce the parental flower-colours, accompanied sometimes by colours not seen in the parents, together with the purple or pink form of the first cross when either occurred.

10. Crosses between parents of different seed-colour, brown and green, showed green to be frequently dominant. Deviations from this general result occurred with certain types used.

11. In certain combinations there was close correlation between (*a*) green colour of seed and hoariness, (*b*) brown colour of seed and glabrousness. *In other combinations, such correlation was entirely wanting.*

12. The rule that plants with flowers, either purple or claret, arose from green seeds was universal. For seed-colours of the pure white types, see pp. 33 and 34.

13. When glabrous plants were produced by the first cross, they were found to be pure recessives, and their colour was that of their recessive parent. Such plants were always the offspring of recessive *seed* parents, and there is therefore suspicion of self-fertilisation. But with the most punctilious care, such recessives repeatedly occurred when certain strains were used, and in crosses with other strains they were uniformly absent.

Taking all evidence together, we incline to believe that these glabrous first-cross offspring were examples of the "false hybridism" of Millardet (see p. 154).

14. The fact stated in 3, that in certain subsequent crosses individuals occurred which were apparently pure dominants, seems to indicate that similar "false hybrids" may occur of pure *dominant* form also.

15. Speaking generally, the results here detailed agree well with those of Correns. But owing to the use of a large number of types,

our results are necessarily much more complex. It should also be noticed that none of our experiments are precisely comparable with that of Correns, who used a biennial hoary type with purple flowers and a biennial glabrous type with flowers "yellowish-white" (or "sulphur-yellow" of Haage and Schmidt). We used no *biennial* glabrous form.

16. In regard to almost every character studied, the behaviour of several of the different types, strains, and even individuals showed special peculiarities.

The reader who has followed the evidence in *Matthiola* will have seen that the phenomena largely conform to the Mendelian principles. Distinct classes of unconformable phenomena occur, and a few quite irregular cases. These several results cannot be adequately presented in a summary, but in the following tables (Tables XIV and XV) an attempt has been made to give a concise statement of the general results obtained from the various experiments.

Of these twelve aberrant cases (Table XIV), nine we may presume were examples of the "false hybridism" of Millardet. For in these unions, contrary to expectation, a mixed offspring was obtained; but the recessive plants, so produced, bred true—all the offspring obtained from them by two generations of self-fertilisation exhibiting the recessive character. Of actually unconformable, and at present unexplained cases, there remain three; viz.:—

One experiment (10) in which two individuals of the half-hoary type, raised by two generations of self-fertilisation, and crossed with a strain of glabrous plants similarly raised, produced offspring which were all R, when the expectation was all D.

And two experiments (79, 80) in which two glabrous individuals (extracted recessives), crossed with two glabrous strains (recessives raised by two generations of self-fertilisation), produced 94 D and 1 R, when the expectation was all R.

The brief summary of results in Table XV shows—

(1) That in the Mendelian cases the deviations from the exact result are sometimes in the one direction (deficiency of D), sometimes in the other (deficiency of R).

(2) That the aberrant cases *where the expectation is* 1 D : 1 R only include a single instance in which there was a successive use of R parents of *similar* flower-colour (one mating in Experiment 73). In all the other aberrant cases the recessive parents successively employed were of *dissimilar* flower-colour.

(3) That *where the expectation is* 3 D : 1 R, the contrast between Mendelian and aberrant cases is less sharp. No wholly consistent grouping of these aberrant cases appears possible, but the following general statements may be made:—

Table XIV.—Unions in which the expectation is an *unmixed* offspring.

Mendelian Cases.

Results obtained when the expectation is all D.			Results obtained when the expectation is all R.		
Reference number of experiment.	Result.	How obtained.	Reference number of experiment.	Result.	How obtained.
1—9, 11—18	1250 D	From various crosses D × R ..	58*c*—*e*, and others not numbered (p. 79)	1148 R	From self-fertilisation of extracted R's.
19, 20*, 21*, 22*, 24, 25, 27—33, 36, 37, 45, and in part 20, 22, 23, 25*, 35, 39, 40, 42, 46	796 D All D (see experiments)	,, ,, ,, R × D ..	Not numbered (p. 79)	218 R	From self-fertilisation (for one generation) of R's produced in a first cross.
Not numbered (p. 38) ..	148 D	,, ,, ,, (R × D) × D	Not numbered (p. 79)	113 R	From self-fertilisation (for two generations) of R's produced in a first cross.
56*b*, 103*b* 104, 105, 106*b*, 107*b*	979 D	From self-fertilisation of extracted (presumably pure) D's	58*a*—*b*	639 R	From crossing extracted R's with R's resulting from self-fertilisation.

Aberrant Cases.

When the expectation is all D.			When the expectation is all R.		
Reference number of experiment.	Result.	How obtained.	Reference number of experiment.	Result.	How obtained.
10	72 R	From [(D × self) × self] × [(R × self) × self]	79, 80	94 D 1R	From crossing extracted R's with R's resulting from self-fertilisation.
(In part) 20, 22, 23, 25*, 35, 39, 40, 42, 46	Mixed D and R (see experiments)	From various crosses R × D ..			

Table XV.—Unions in which the expectation is a *mixed* offspring.

Mendelian Cases.

Ratios obtained when the expectation is 1D : 1R.		
Reference number of expt.	Ratio.	How obtained.
	D : R.	
85	1 ·19 : 1	From the cross $(R_1 \times D) \times R_1$
86	·98 : 1 (neglecting unsown seeds)	,, ,, ,,
91	·84 : 1	,, ,, $(R_1 \times D) \times R_2$
49	·99 : 1	,, ,, $(D \times R_1) \times R_2$
50	1 ·13 : 1	,, ,, ,,
59	·86 : 1	,, ,, ,,
65	·94 : 1	,, ,, ,,
52	1 ·13 : 1	,, ,, $[(D \times R_1) \times R_2] \times R_2$
53	·85 : 1	,, ,, ,, ,,
69	·91 : 1	,, ,, ,, ,,
70	1 ·00 : 1	,, ,, ,, ,,
71	·81 : 1	,, ,, ,, ,,
74	·90 : 1	,, ,, ,, ,,
73*a*	1 ·01 : 1	,, ,, ,, ,,
76*b*	1 ·04 : 1	,, ,, ,, ,,
? 72	1 ·00 : 1	,, ,, ,, ,,

Average ratio.............................. 1 ·03 D : 1R.
Ratio calculated from the sum of the totals.... 1 ·03 D : 1R.

Ratios obtained when the expectation is 3D : 1R.		
Reference number of expt.	Ratio.	How obtained.
	D : R.	
68	2 ·98 : 1	From self-fertilisation of $(D \times R)$
92	3 ·05 : 1	,, ,, ,, $(R \times D)$
93	3 ·83 : 1	,, ,, ,, ,,
94	3 ·00 : 1	,, ,, ,, ,,
55	2 ·92 : 1	,, ,, ,, $[(D \times R_1) \times R_2]$
84	2 ·90 : 1	,, ,, ,, $[(R_1 \times D) \times R_2]$
98	3 ·13 : 1	,, ,, ,, ,,
99	3 ·22 : 1	,, ,, ,, ,,
100*b*	2 ·51 : 1	,, ,, ,, ,,
101	3 ·16 : 1	,, ,, ,, ,,
103*a*	2 ·65 : 1	,, ,, ,, $[(R \times D) \times \text{self}]$
106*a*	4 ·00 : 1	,, ,, ,, ,,
? 102*b*	4 ·00 : 1	

Average ratio .... 3 ·18 D : 1R.
Ratio calculated from the sum of the totals.... 3 ·22 D : 1R.

Table XV—*continued.*

Aberrant Cases.

Results obtained when the expectation is 1D : 1R.			Results obtained when the expectation is 3D : 1R.		
Reference number of expt.	Result.	How obtained.	Reference number of expt.	Result.	How obtained.
87—90	All D or almost all D	From the cross— $(R_1 \times D) \times R_2$	100*a* 102*a*	All D	From self-fertilisation of— $[(R_1 \times D) \times R_2]$
60—63	,, ,, ,,	$(D \times R_1) \times R_2$	51, 54, 56*a*, 66, 67, 81— 83, 97	Offspring mixed ; 1·8D : 1R	$(D \times R)$ in 3 cases $[(R \times D)$ in 1 case$]$ $[(D \times R_1) \times R_2]$ in 4 cases $[(D \times R) \times \text{self}]$ in 1 case
75, 76*a*	,, ,, ,,	$[(D \times R_1) \times R_2] \times R_3$			
73*b*	All D	$[(D \times R_1) \times R_2] \times R_2$	95, 96, 107*a*	,, ,, 4·7D : 1R	$(R \times D)$ in 2 cases $[(R \times D) \times \text{self}]$ in 1 case

(α) That in the two cases in which recessive offspring were altogether absent (Experiments 100*a*, 102*a*), the experiments were of a parallel nature, the dominants in each case arising from the operation $[(R_1 \times D) \times R_2] \times$ self.

(β) That in all such cases (except Experiment 102*a* mentioned in (α)) where the dominant type introduced in the first cross had been one of the annual forms 2, 3*a*, 3*b* (Experiments 51, 54, 66, 67, 81, 82, 83, 97), the proportion of dominants was invariably too low (1·8 D : 1 R). In fact, this aberrant result was universal for all such experiments with the types 2 and 3*a*. Type 3*b*, however, gave a Mendelian result in the two other similar experiments (Experiments 55, 84).

(γ) That in all such cases (except Experiment 100*a* mentioned in (α)), where type 1 had been originally used as a dominant pollen parent, the proportion of dominants was invariably too high (4·73 D : 1 R) (Experiments 95, 96, 107).

[In neither (β) nor (γ) were the operations of precisely the same form as in (α).]

[Note, added March, 1902.

The Aberrant Results obtained from Cross-breds.

Frequent mention has been made of the fact that cross-breds when fertilised with the original recessive, gave Mendelian equality; while when fertilised with a new recessive, they gave all or nearly all dominants. It has been also stated that self-fertilisations in several cases similarly showed the gametes of these individuals to consist of dominants and recessives in the usual proportions.

At first sight it seems impossible to provide a rationale of such cases. One hypothesis, however, suggests itself, which however improbable, is not yet excluded. This suggestion in fact is, that the excess of hoary offspring produced by the cross with the second recessive may actually have been formed by the union of dissimilar gametes, both bearers of the glabrous character. Were this the case, it would be one more example of a "reversionary" form being assumed as a heterozygous character (see p. 144).

The peculiar results obtained in Experiments 73*b*, 79, and 80 are conceivably explicable on the same hypothesis, but it must then be further supposed in those cases that further resolution of the primary character has taken place.

Unfortunately no cross has yet been made between two pure glabrous types, but Messrs. Haage and Schmidt, of Erfurt, have, in reply to questions, most kindly given us their experience in the matter. This is to the effect that crosses between glabrous varieties of *dissimilar* colour may give hoary plants, but very rarely, not more than 1 in 1000 perhaps. In view of their evidence the suggestion here made is exceedingly remote, but some reference to this obvious possibility is called for.

In considering the other aberrant group of cases where cross-breds on self-fertilisation gave too high a proportion of recessives with some consistency, the possibility of "false hybridism" on the recessive side should not be forgotten.]

PART II.—POULTRY.

Experiments begun in 1898, *carried out by W. Bateson.*

The two breeds first chosen for experiment were Indian Game and White Leghorn. Experiments were subsequently made with Brown Leghorn, White Dorking, and with a single white Wyandotte hen.

Indian Game are dark birds with yellow legs and pea combs. By a "pea comb" is meant a comb consisting of three fairly regular longitudinal ridges, along each of which are several more or less lumpy tubercles. In both sexes the pea comb is low, that of the cock rising about 1 to 1½ inch from the skull, while that of the hen is only about ¼ to ½ inch high, being in fact rudimentary. In the hen the tubercles may be almost entirely suppressed. Any one who desires to examine such combs can see them any day in a poulterer's shop. From the "single" comb of the Leghorns the pea comb is readily distinguished by the absence of sharp serrations, and by the presence of the lateral ridges (often obliterated in old hens).

In correlation with the low comb, the wattles are also very short, being almost rudimentary in the hen, and only about 1 inch long in the cock. The ear-lobes in both sexes are bright red, like the wattles, but they project very slightly, and though a little full below, they are never pendulous, as in the Leghorn cock.

The plumage of the cock is for the most part black, shot with dark green. The hackles and saddle are broken with a variable amount of dark red, which if noticeable, is considered by the fancier a fault. There is a large brown patch extending across the secondaries.

The plumage of the hen, with the exception of the hackles which are black, is almost entirely composed of black and brown mixed together in almost every feather. The mixture should be in the form called "lacing" (concentric lozenges or rings of colour), which may be either single or double, in the various parts of the body. The quill-feathers are liable to be vermiculated or "mossed" with brown, which is also reckoned a fault.

The details of coloration are complex, but for our purpose need not be described. There is a good deal of variation between strains as regards minor points, but on the whole the breed is a very uniform one.

The down of the newly hatched chicks may be *either* striped dark and light brown, *or* almost entirely without dark stripes, leaving the general colour then a nearly uniform buff. All intermediates may occur, but in individual families there is often a fairly sharp discontinuity in respect of down-coloration, though the birds when grown up may be quite alike.

To the eye, a most striking feature in these birds is the close, "hard" feathering, and upright carriage. It is to the closeness of the feathering that is largely due the appearance of great length of neck and leg, which constitute a prominent character.

The shanks are, in healthy and well-grown birds, of a full deep yellow. In depauperated specimens they are a more dingy yellow.

The bill is either a deep yellow or of a rather dingy horn-colour. Black pigment is not in my experience found in the shanks of pure-bred birds, but there may be a good deal of pigmentation in the bill, especially in cocks.

The eggs are brown, varying in individual birds from a full dark brown to a very pale *café-au-lait.* The colour of the egg varies irregularly with the health of the bird and with the rapidity with which the eggs are being produced, getting paler when eggs follow each other with abnormal rapidity and towards the end of a batch. The number of eggs produced is very small in comparison with most breeds: the hens are good sitters and mothers.

As to the origin of Indian Game I can obtain no certain information. In this country the breed has come into prominence only within the last twenty-five years. It is no doubt closely connected with the Aseel and Malay breeds, but whether it was imported as an already established breed, or whether it has been produced in this country, is not certain. The breed was, and still is, chiefly kept in Devonshire and Cornwall, but now it is widely spread. To those unfamiliar with poultry, it may be mentioned that Indian Game is a breed thoroughly distinct from ordinary Game fowls.

Whatever be its origin, Indian Game breed now as true to their chief characteristics as any other breed. When two pure strains are crossed, the offspring frequently show white patches on the secondaries, and the comb may increase in size,* taking the form here called "intermediate pea." This comb has the three ridges well marked, but the extent upwards from the skull is in the cock about 2 inches, and in the hen about $\frac{3}{4}$ of an inch. The intermediate pea in the cock usually falls over to one side. Such a comb would be considered a great disfigurement, but it certainly may occur in good strains. It should be mentioned that the cocks are generally dubbed for exhibition, and consequently the details of comb structure have not been much attended to by fanciers.

For our purpose it is important to notice that the true pea comb and the intermediate pea are hardly if at all distinguishable *in the newly hatched chick.* The distinction does not become evident, especially in females, until sexual maturity approaches. At all ages both are readily distinguishable from the single comb of the Leghorns.

White Leghorns.

The other breed originally chosen was *White Leghorn.* Leghorns as a definite breed are probably at least 50 years old, and at the present time exist in many colours which breed fairly true. One of the most definite is the white breed, which can be absolutely relied on to propagate itself without notable variation.

The comb is a high single comb, with one row of large serrations of varying number, including at least four or five large points distinct from the more or less irregularly divided anterior and posterior lobes. In the cock the comb is erect. Measured from the skull to the tip of the serration next over the eye, the height in an adult is 3—4 inches, varying in actual size both with age, treatment, and condition. In full-grown cocks it projects forwards over the bill and backwards behind the head, the total length being about 5 inches. Fine prize birds in show condition may considerably exceed these measurements.

In the hen the comb is similar though smaller, usually lying over to one side, the correct position in the fanciers' opinion. The size in hens varies a good deal in individuals, and greatly with condition. About 2 inches high and 3 inches long may be given as average dimensions, greatly exceeded in breeding condition in some cases. In correlation with the high comb, the wattles are long, reaching in the cock to a length of some 4½ inches from the angle of the gape. In the hen they are about 2 inches long. The ear-lobes are bluish or yellowish-white and pendulous, increasing in size greatly with age.

The plumage is entirely white, without the least speck of any colour. It is *never* close-fitting as in Indian Game.

Legs and bill are pale yellow. The older females frequently (? in all strains) have large spurs without any decline in fertility. The eggs are white, and produced in great numbers. The hens do not as a rule sit or show any sign of broodiness.

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* This has been my experience, but I am not sure if the fact is generally true.

These breeds seemed specially suitable, because they differed from each other in their combs, a structural character. The great apparent difference in proportional length of leg bones, which at first sight seemed capable of measurement, proved on examination to be due almost entirely to the difference in closeness of feathering, the loose feathers of the Leghorns altering the general outline of the body, and making the legs appear shorter by comparison.

A special reason for choosing these two breeds, apart from the general suitability, was that it was possible to obtain birds of each, with a statement as to their immediate pedigree. The stock of Indian Game was supplied by the Rev. E. P. Boys-Smith, vicar of Hordle, Lymington, Hants, who had bred them with care for some years, keeping careful pedigrees. The original White Leghorns came from Mr. E. C. Lister-Kay, of Burley Manor, Ringwood, Hants, and of them also I was given a pedigree, carefully kept though incomplete as regards the individual identity of the hens, several sister hens being run with one cock. Both these gentlemen have supplied many practical hints and information, which have proved most useful.

In the first two years of experiment many troubles occurred, mostly owing to overcrowding and errors arising from inexperience. Consequently the results obtained were on a small scale. A more serious difficulty was caused by the loss of so many chickens in the spring that the thoroughbred strains had largely to be represented by late-hatched birds, a source of difficulty if not actual error, for it is not unlikely that heredity results may differ with health.

LIST OF ORIGINAL BIRDS.

The following is a complete list of the birds introduced for the purpose of these experiments, with the abbreviations which will be used hereafter to distinguish them :

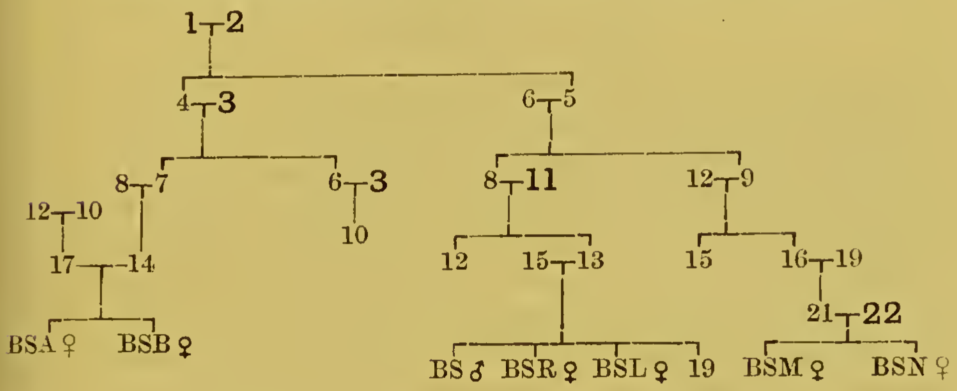
INDIAN GAME.

1. Cockerel and two pullets, own brother and sister, in-bred, from the Rev. E. P. Boys-Smith (BS ♂, BSR ♀, BSL ♀).

2. Two pullets, own sisters, in-bred, related to the above (BSA ♀, BSB ♀).

The above two lots were collaterally related, but showed features of slight difference in colour and build. Both were about equally in-bred. The actual details of the pedigree are complicated, and though little importance may be attached to the details of relationship, I subjoin the pedigree for future reference if required. The extent to which the birds were in-bred may be gathered from the fact that in seven generations only four unrelated birds occur, and the last introduction of fresh blood, or the hen which stands as great-grandmother to one lot and grandmother to the other. The mating generally used was nephew and aunt.

Pedigree of Indian Game Birds received from Mr. Boys-Smith.



In the above pedigree the male is on the left side in each mating. The Clarendon figures show the introduced birds. No doubt all are in some degree related, as the best strains are in few hands.

3. Two hens, full sisters, from Mr. Boys-Smith, sent in 1901, being then in their second breeding season. These are indicated in the pedigree as BSM ♀ and BSN ♀.

4. Cockerel and pullet from the Rev. C. T. Bromwich (Brom. ♂ Brom. ♀). As to the pedigree of these birds, no account was to be had, but it was said that a new male was introduced each year in their immediate pedigree, and the birds bought were almost certainly either full or half brother and sister. As will be seen hereafter, there is doubt as to whether these birds were "pure" in the critical sense.

5. Cockerel of unknown extraction from Ringwood Poultry Farm. (Rd. IG ♂.)

6. Cockerel of unknown pedigree from a Lancashire breeder. (Gr ♂.) The question of true "purity" is also doubtful in this case.

WHITE LEGHORNS.

(*For description see above.*)

1. Cockerel and pullet from Mr. Lister Kay, not in-bred. (LK ♂, LK ♀.)

From a fancier's point of view these birds were not in-bred at all;

for in their pedigree a fresh cockerel, presumably unrelated, was introduced at each successive generation.

2. Cockerel and three pullets hatched from eggs purchased from Mr. Adeane, Babraham Hall (Babr. ♂, Babr. ♀ 42, Babr. ♀ 89, Babr. ♀ 110). These birds were almost certainly not in-bred. They came from a run where many cocks and hens were together, and it is unlikely they were nearly related to each other, though this may have been the case.

3. A pullet from Ringwood Poultry Farm (Rd.L ♀).

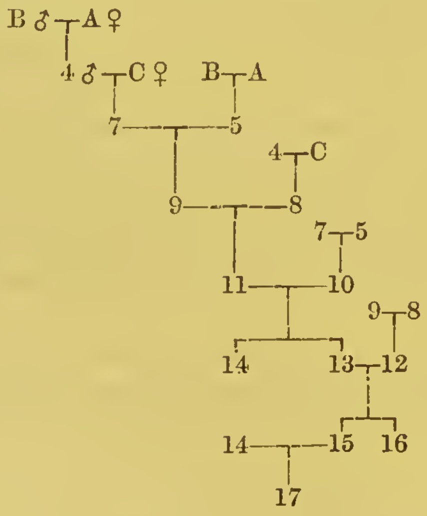
BROWN LEGHORNS.

1. A pullet from Mr. Boys-Smith, sent me in 1900 (Br. L^1).
2. A sister to the foregoing sent in 1901 (Br. L^2).
3. A cock sent in 1901, nephew to the foregoing (Br. L ♂).

As regards structural characters, Brown Leghorns closely resemble White Leghorns. In colour of plumage the browns have bright golden-red hackles, red coverts and saddle, with black breast, quills and tails in the cocks, while the hens are of a duller general mottled-brown colour, the hackles being golden yellow, with black central stripe. The breast is a bright chestnut. The deaf ears are white in all Leghorns,* and the bills and shanks are yellow. Eggs white. Hens do not sit. These birds were closely in-bred, as the following pedigree will show :—

Pedigree of Brown Leghorns.

A ♀, B ♂, C ♀ were three unrelated birds.



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* Dr. W. T. Blanford has called my attention to the interesting fact that the *G. bankiva* of Burmah differs from that of India in having the ear-lobes or "deaf ears" red instead of white, and has given me the following references on the subject: Blyth, 'Ibis,' 1867, p. 154, and 'Fauna Brit. India,' "Birds," vol. 4, pp. 76—7.

Here No. 17 represents Br. L ♂, and No. 16 the two hens, Br. L 1 and 2. The usual mating is again aunt and nephew. (Father on the left in each mating.)

WHITE DORKINGS.

The White Dorking is a pure white bird with white bill and shanks, and a *rose-comb.* The feathers are loose-fitting, and never close-fitting. A rose-comb consists of a great number of papilliform elevations, standing in the same horizontal plane. It is wide in the middle, and contracts to a point or "pike" behind.

It is recognisable at an early age in embryonic life, and can never, from about the 9th day of incubation, or earlier, be confused with a single comb. The distinction between rose and single is, with the rarest exceptions, absolute, and no class of intermediates needs here to be distinguished. The rose comb rises about 1¼ inches from the skull in cocks and rather less in hens which are laying, while in hens out of breeding condition, it scarcely rises from the head more than half an inch.

The wattles are about 1½ inches long in cocks, and about 1 inch long in hens. They are rounded in shape. The deaf ears are red and project but little, never being to any extent pendulous.

The bill and shanks are pale pinkish-white, without pigment. The breed has the extra or fifth toe, characteristic of all Dorkings. The eggs are long, of a faint stone-colour, and the hens go broody.

WHITE DORKINGS.

1. Two pullets received from Mr. O. Cresswell, Morney Cross, Hereford, in 1901 (Cr 121 and Cr 122). In Cr 121 a faint tinge of chestnut appeared on one secondary of each wing after the moult of the second year (see p. 98).

2. A cockerel received at the same time from the same source. (Cr ♂.)

3. A pullet received from Miss Knowles, Conholt Park, Andover, in 1900 (K ♀).

4. A cockerel from the same source (K ♂).

From the two birds K ♀ × K ♂ were raised two pullets, Dork. 262 ♀, Dork. 263 ♀, and one cock, Dork. 258 ♂.

Though I have no pedigree with either of these lots, Mr. Cresswell informs me that his birds are very closely bred, but the details are unknown. The breeding of Miss Knowles' birds is also unknown, though in all probability they are not specially in-bred. These two strains are only remotely related. As will appear, it became practically certain later that one (? both) of the K birds was not pure in respect of rose comb. In reply to an inquiry, Miss Knowles was so good as to send information that single combs appear occasionally among her chicks, perhaps 1 in 30, especially when fresh blood is introduced, confirming the view here given. The bearing of these facts will be considered later.

White Wyandotte.

The Wyandotte is another loose-feathered rose-combed breed, but the comb differs from the rose of the Dorking in the fact that the posterior point is directed slightly *downwards* instead of backwards. For our purposes the only other feature of importance is that the deaf ears are round and red, and the bill and shanks yellow. The white variety is not a well-recognised breed, and I know nothing of it beyond the fact that I obtained such a pullet from Ringwood poultry farm. Pedigree unknown.

Before giving the details of specific experiments, it will be useful to state in general terms the results when the various breeds are crossed together. Except in regard to the distribution of pigment in the White Leghorn × Indian Game crosses, reciprocal unions do not differ in result.

Crosses between White Leghorn and Indian Game: General Account.

1. *Comb and Wattles.*—In the cross-bred the comb is almost always *either* a true single comb, frequently but not quite always differing from the pure Leghorn by diminution in size; *or* an intermediate pea. Of the latter there are many degrees.

The distinction between the single and any form of pea comb is *in almost every case* immediately recognisable in the chicks at hatching, and indeed some seven days before. The single comb in unhatched chick lies as a sharply serrated flap of skin folded down on the head, while the pea comb consists of tubercles slightly rising from the skin. In later life the distinction between intermediate and single may become less obvious; but even though the comb may grow up to some height, the three ridges of the pea comb remain marked. The intermediate pea-comb in adults of both sexes usually lies over to one side or the other, like that of the Leghorn hen.

As the sequel shows, the appearance of these two kinds of comb in the first crosses connotes two wholly distinct phenomena; for, while the pea comb is an ordinary dominant DR, the single is a recessive, and *cross-breds with single combs proved incapable of transmitting the pea comb.*

The development of the wattles is closely correlated with that of the comb. Long wattles are associated regularly with a large comb. Owing to the great changes in size to which these structures are subject, according to the state of health, they are not characters suited to very precise measurement.

2. *Plumage-colour.*—Of the hundreds of crosses made both ways, all, with one single exception, were white or dingy white* coloured birds, more or less speckled or "ticked" with black. Such ticking is rarely extensive, and is quite irregular and asymmetrical. The ticking may affect parts of feathers, single feathers, or small patches of feathers.

The ticks may be either plain black, or disposed as barrings or chequerings, especially in hackles and saddle-feathers.† The details of these markings have probably some significance, and may perhaps be described on another occasion.

In addition to the dark ticks the cocks not rarely have patches of reddish or brown colour ("pile") on the wing-covers and saddle rarely as developed as in pile breeds. Such brown marks occur occasionally in hens, but are very small. The brown marks may rarely be barred or chequered.

In respect of ground-colour reciprocal crosses give the same result in *male* offspring. All male cross-breds, and *female* cross-breds *from Indian Game mothers*, have the ground-colour *white*, but *female cross-breds from White Leghorn mothers* almost always have the ground-colour more or less dingy brownish-white. The dinginess is sometimes hardly noticeable, but occasionally it is so striking as to make the bird look a dirty cream colour. It is clearly due to a general deposition of a very fine layer of pigment. Such "dingy" hens, though ticked as the others are with pure black, *never have barred or chequered* feathers, so far as our experiences goes.

In the dingy hens the skin of the face is generally somewhat pigmented, though in various degrees, sometimes approaching to the "purple-face" of Brown-breasted Game and other breeds. No dinginess was ever seen in a male bird.

3. *Bill and Shanks.*—These are full yellow, except in "dingy" hens. In the latter there is pigmentation irregular in amount, varying in the case of the shank from slight patches to a general dark olive. The soles of the feet are always yellow. The bills of dingy hens are striped asymmetrically and irregularly with black or brown. The degree of blackness in shanks is correlated with that in bill fairly closely. This pigmentation begins when maturity is approached and cannot be detected in the shanks of young chicks. Of all the female cross-breds with I.G. fathers which reached the age for pigmentation, only one failed to exhibit it either in bill, or shanks, or in both.

4. *Deaf Ears.*—These are usually patchy, partly red and partly

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[*] The exception was an extraordinary piebald chick which died young. The middle of the back was occupied by a large irregular island of striped colours, like those of a normal Ind. Game chick. This patch extended asymmetrically on to the proximal parts of the limbs.

[†] These barred feathers were noticed by Darwin in poultry crosses ('Animals and Plants,' Ed. 2, vol. 2, p. 255), and regarded by him as reversionary.

white, showing a mixture of the parental characters both in colour and shape.

5. *Carriage.*—The attitude of the crosses is much more like I.G. than Leghorn. Though not so "reachy" as a fine Indian Game, they never have the general appearance of Leghorn. This appearance is doubtless due to the fact that the hard, close feathering of the I.G. is always in some degree dominant.

6. *Eggs.*—The shells are usually of intermediate tint. Eggs brown enough or white enough to pass for pure I.G. or pure L. are decidedly rare.

7. *Broodiness.*—Many of the cross-breds became broody and made fair mothers. Some were very uncertain, but perhaps not more so than many hens of sitting breeds. Some did not go broody at all.

In regard to colour of eggs, fertility, and broodiness, for want of opportunities no extensive observations were made.] Moreover, for any adequate study of most of the other points enumerated, it is necessary that the chickens should be reared to maturity. To do this with large numbers is quite beyond our resources. Fortunately, however, the comb-structure can be determined with certainty in very young chicks at about the 14th day of incubation. By the use of this fact the range of available statistics has been greatly increased. For by opening the eggs on the 15th day, the same incubator can be filled more frequently, and the serious expense of raising many hundreds of chickens is so far dispensed with.*

As stated above, the single comb is always single and can be recognised as such from an early stage. Besides variations in size and straightness, single combs sometimes have as a defect one or two lateral processes or "sprigs" at the hinder end. This is a fault to which the best strains are occasionally liable. The pea comb in cross-breds varies greatly as described, ranging through many intermediate forms towards the single comb.

In counting chickens as pea-combed, it will be understood therefore that most of them would undoubtedly have had *intermediate* pea combs on reaching maturity, but none would have had single combs. An attempt was made at first to distinguish pea combs from intermediate pea combs, but this was afterwards abandoned as unreliable. Latterly when the eye became trained, it was fairly easy to recognise cross-bred pea combs (DR) from pure peas (DD), at all events in cocks from the first, but the hens are much more difficult.

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* When, in these results, the numbers of cases recorded for comb, foot-character, or colour differ, it must be understood that for some reason one or more specimens were only available for certain determinations. For example, a certain number of chicks which died too early (generally about the 10th day) for the comb- or colour-character to be made out with certainty, might show the foot-characters perfectly; in such a case the one character is reckoned and the others are left undetermined. Consequently there is sometimes, as in Experiments 37 and 38, an apparent discrepancy between the numbers given for comb or foot character taken separately, and those given for both in combination.

First Crosses between Brown Leghorn and Indian Game: General Account.

Only a small number of birds of this cross have been reared to maturity, namely, five cocks and eight hens, the offspring of one Brown Leghorn hen and two Indian Game cocks; and one cock bred reciprocally. These cross-bred birds had dark plumage, which may be sufficiently described as compounded of the parental colours and forms: bill, horn colour; legs, yellow; ear-lobes, white tinged with yellow like Leghorn, feathering and carriage intermediate, but nearer to the Game; comb and wattles as in the crosses between Indian Game and White Leghorn.

White Leghorn with White Rose-combed Dorking.

The offspring is always white. The bill and shanks are white like the Dorking, or rarely with a faint tinge of yellow.

In point of carriage and disposition of feathering the two parent forms are so nearly alike, that for our purposes these characters cannot be used as a criterion of inheritance. Deaf ears usually red, or red patched with white, in shape intermediate.

The comb is *either* single as in Leghorn, differing only in reduced height, *or* rose as in the Dorking; but often raised from the head rather more than in the normal form. Wattles follow the comb closely. Some have and some have not the extra toe;* details given later.

As regards characters appearing in later life, such as egg-colour, breeding habits, spurring of hens, &c., the numbers reared to adult life were insufficient to warrant a statement.

In the great majority of cases the extra toe is *either* palpably present as a distinct digit *or* absent. When present the two hind toes may consist, as in the normal Dorking, of a short toe like the hallux of a 4-toed bird, with a long many-jointed digit proximal to it pointing upwards. The two, however, may often be *both* short, pointing downwards, never both long. This condition ranges through many stages of bigemination down to mere bifidity of the nail. A form very rarely seen is an *elongation* of the hallux without any extra toe being present.† In such a hallux there is increase in the number of phalangeal joints. This of course corresponds to the three-jointed pollex in man. More or less complete webbing is common in cross-breds.

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* This foot-character can be sufficiently made out in chicks after about 12 days of incubation.

† [A chick has lately occurred with *such a "long" hallux bigeminus*—probably a hitherto unrecorded form.] March, 1902.

In the highest form of the reduplication the short toe is itself also represented by two digits, making six in all. Of this, also, there are many grades.

Lastly, any of these conditions may be seen on one foot only, while the other foot shows one of the other states or is normally four-toed. Generally speaking, however, there is a fairly close symmetrical agreement between the two feet.

Some of these phenomena have been referred to by many writers,* and a full description could only be given in a separate treatise. For our purposes all the several states indicating digital proliferation in the region of the hallux are counted as "extra toe," inasmuch as they all show the existence of the condition if in varying degrees. When this condition is shown on one foot only, the bird is reckoned with the extra-toed, but the fact is stated.

Brown Leghorn and White Rose-combed Dorking.

Nearly white in general colour of plumage, but with ticks and splashes almost exactly as in the Indian Game—White Leghorn crosses. Otherwise like the White Leghorn—White Dorking crosses.

To the statement in regard to colour the birds bred in Experiment 25 form an exception. Of twenty-two such chicks, four were dark, two were doubtful, and the remainder light. Only two of the darks were reared, and one was like a *dark* Dorking dappled with white, while the other turned out a nondescript brown. It will be remembered that Cr 121 had two chestnut feathers, and must be regarded as, to some extent, DR in point of colour (see pp. 105, 112, and 141).

White Leghorn and White Wyandotte.

Of the latter breed only one hen was used. All her chicks by four different White Leghorn cocks were white birds, slightly ticked in some cases, with yellow legs and bills; having rose combs pointing downwards behind, as in the Wyandotte, though rather higher from the skull; wattles to correspond; deaf ears, reddish patched with white. In general shape like the Wyandotte, laying pale stone-coloured eggs like her, and like her exceptionally fertile. In the pure Wyandotte the eggs should be brownish.

On a survey of the various characters enumerated it at once appears that the distinction between the various kinds of comb, and the distinction in regard to presence or absence of the extra toe, inasmuch as they exhibit a fairly sharp discontinuity, are characters well adapted to statistical treatment. As has also been stated these distinctions can be perceived from an early age in the young chick, so that much larger statistics can be obtained in regard to them than as to the other characters. In what follows, therefore, primary regard is had to these characters, though some important considerations arising out of the other characters must also be considered later.

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* References in 'Materials for the Study of Variation,' p. 390.

Indication of the Mendelian Laws.—Description of the detailed results may be greatly facilitated if we anticipate the recital of experiments, and state at once that in a considerable group of the crossings the operation of the Mendelian laws can be perceived. This group will be considered first, and for convenience will be referred to as the Mendelian group. Many complications must be dealt with, but so far nothing conflicts with the main result.

The cases grouped as Mendelian all show clear dominance. By speaking of the remainder as non-Mendelian it is not suggested that the heredity is not in accordance with the Mendelian principles; but merely, that as there is a condition more complex than that of simple dominance, the application of the Mendelian principles cannot be clearly followed out.

Using the Indian Game birds of

Sections 1 and 2, and their direct descendants ...	p. 90
Section 3..	p. 91
The hen of Section 4	p. 91
The cock of Section 5	p. 91
The Dorkings of Sections 1 and 2......................	pp. 91 and 92
and the Wyandotte hen.................................	p. 94

with any of the Leghorns, male or female, the facts show that

pea comb,
rose comb,
extra toe*

are *dominant* characters, and that

single comb,
the normal foot

are *recessive* characters.

We are thus provided with a terminology and a *rationale* of phenomena, which when we come to the more complex results will be found a valuable guide.

Purity of Strains.—A word must now be said as to the purity of the strains. When the Mendelian principles are appreciated, purity acquires a new and precise meaning. This we shall subsequently discuss (see p. 134). For the present it will suffice to say that in regard to the various Leghorns, we have no evidence of a bird, the offspring of two Leghorns, having a comb other than single or a foot other than four-toed. With regard to those characters, therefore, the strains must be called pure.

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* The dominance of this character, as will be seen, is not absolute, and a cross-bred without any trace of extra toe may be DR in respect of that character.

Similarly the Indian Games and Dorkings, *just enumerated*, have always produced birds with the comb and foot characters* of their respective breeds, so that in respect of these characters they also were pure. Of the actual numbers of thoroughbreds so produced only imperfect records were kept. They would have added to the completeness of this account; but when the results of the crossings are understood it will be seen that these precise numbers would not have contributed anything of significance. In general terms, however, we may say that these numbers were in each case considerable—say from twenty to fifty.

MENDELIAN GROUP.

Crosses between Leghorns and Indian Game.

Details of Experiments in regard to Comb.

The following lists give the actual numbers of birds with each kind of comb obtained by crossing the parents enumerated on p. 99 with Leghorns. The breeding of the Indian Games is stated in the course of the experiments.

By "1 year," "2 years," &c., after the name of the bird is meant that it was in its first or second breeding season, &c. These and subsequent experiments are numbered consecutively for reference.

				P.c.	S.c.
†1.	I.G. BSA ♀ (1 year)	×	LK ♂ (1 year)	11	0
2.	,, BSL ♀ (2 years)	×	do. (2 years)	9	0
3.	,, BSR ♀ (2 years)	×	Babr. ♂ (1 year)	13	0
4.	,, BSB ♀ (2 years)	×	do. ♂ (1 year)	7	0

From BSB ♀ (one year) × BS ♂ (one year) were bred the following thoroughbred Indian Games—25 ♀, 35 ♀, and 30 ♂, which, mated with Leghorns, gave the following:

				P.c.	S.c.
5.	Babr. 110 ♀ (1 year)	×	I.G. 30 ♂ (2 years)	19	0
6.	Babr. 89 ♀ (1 year)	×	do. (1 year)	15	0
7.	BrL1 ♀ (1 year)	×	do. (1 year)	19	0
8.	Unknown white Lgh. ♀ bred by us, but label lost	×	do. (2 years)	19	0

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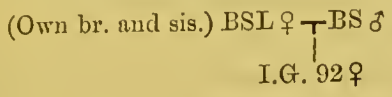
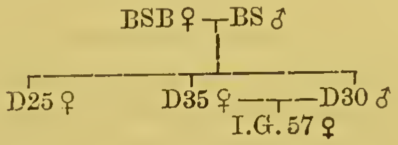
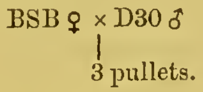
* The extra toes may show occasionally one of the rarer states in these pure-bred birds, but one at least is always present.

† The attempt to cross Legh. LK ♀ with I.G. BS ♂ failed. It was tried repeatedly, sometimes by leaving the two birds for weeks together, at other times putting either in the other's cage. The cock always tore and kicked her, and though he had been kept alone for some days he never trod this particular hen. He was not tried with any other Leghorn.

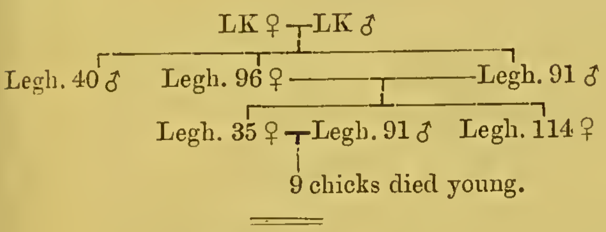
From the original Indian Game of the Mendelian sections, thoroughbreds were raised as follows:

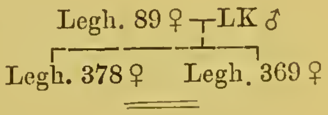


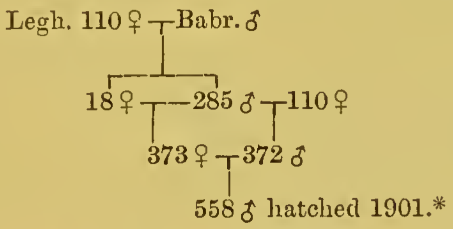


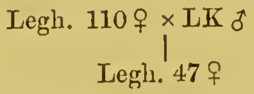


From the original White Leghorns, thoroughbreds were raised as follows:









Using these birds, the following results were obtained:

			P.c.	S.e.
9.	I.G.	35 ♀ (1 year) × Babr. ♂ (1 year)...............	7	0
10.	„	25 ♀ (1 year) × „ (1 year)...............	4	0
11.	„	57 ♀ (1 year) × Legh. 285 (1 year)...........	6	0
12.	„	3 pullets (BSB ♀ × D30 ♂) × Legh. 355 ♂ (1 year)	12	0

All pullets used in Experiments 9—12, were late-hatched the year before, and consequently laid few eggs, apart from any question of effects of in-breeding.

			P.c.	S.c.
13.	I.G.	92 ♀ (1 year) × LK ♂ (2 years).................	18	1
14.	„	„ (2 years) × 91 (LK × LK).................	23	0

From matings 1—14, in some of which the Leghorn was father, in others mother, were produced pea comb 182, single comb 1, so that, with one single exception there was complete dominance of the pea comb.

To these cases of complete dominance we may add the following, in which it must be noticed that Indian Game blood from a new source is introduced. From Indian Game, BSR ♀ × Indian Game Brom. ♂, a family was raised of which some were certainly *not* pure in respect of pea combs. For when bred together some, at least, of them were capable of producing, and did produce, single-combed offspring.

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* The numbers in this pedigree are those by which the birds are spoken of.

This will be fully discussed later, and the relationships of the family tabulated (see p. 112), but at present it may be stated that of this family a pullet and cockerel, own brother and sister, were mated, and produced several chickens, of which two only survived, viz., Indian Game 59 ♂ and Indian Game 120 ♀. Crossed with Leghorns, their offspring were as follows :

		P.c.	S.c.
15.	Legh. Babr. 42 ♀ (2 years) × I.G. 59 ♂ (1 year).....	24	0
16.	„ „ 89 ♀ (2 years) × „ (1 year).....	17	0
17.	Brown Legh. 1 ♀ (2 years) × „ (1 year).....	16	0
18.	Legh. 96 ♀ (1 year) × I.G. 59 ♂ (1 year)	24	1 doubtful
19.	„ 35 ♀ (2 years) × „ (2 years)...........	15	0
19*a*.	I.G. 120 ♀ (1 year) × Legh.LK ♂ (3 years)	7	0

In all, therefore, these two I.G. birds produced 103 p.c., 1 doubtful s.c.

The other Mendelian Indian Game gave the following results :

		P.c.	S.c.
20.	I. G. Brom. ♀ (1 year) × Legh.LK ♂ (1 year)	18	0
21.	Legh. Babr. 89 ♀ (1 year) × I.G. Rd. ♂ (2 years)	29	1
22.	I.G. BSN ♀ (2 years) × Legh. 373 ♂ (1 year)	37	1
22*a*.	„ „ (2 years) × Brown Legh. ♂ (2 years)........	34	2
23.	„ BSM ♀ (2 years) × Legh. 369 ♂ (1 year)...........	54	0

From these 25 matings, therefore, were produced 457 p.c., 5 s.c., and 1 doubtful.

Crosses between Leghorns and White Dorkings.

Details of Experiments in regard to Comb and Feet. (*Mendelian Group.*)

		R.c.	S.c.	E.t.	1 e.t.	No e.t.
24.	Cr ♀ 121 (1 year) × Legh. 285 ♂ (2 years)	12	0	12		0
25.	„ (2 years) × Brown Legh. ♂ (2 years)	22	0	16	4	2
				(see below, p. 113)		
26.	Cr ♀ 122 (1 year) × Legh. Babr. ♂	25	1	18		0
27.	Legh. 18 ♀ (1 year) × Cr ♂ (1 year).....	23	0	23		0
28.	Legh. 96 ♀ (2 years) × „ (2 years)....	20	0	20		0
29.	Legh. 47 ♀ (1 year) × „ (1 year)	21	1 inter.*	21	1	0

Taken together, therefore, 2 White Dorking hens with 3 Leghorn cocks gave 59 rose combs and 1 single, while 3 Leghorn hens by the same Dorking cock gave 64 rose combs and 1 doubtful. As regards toe, matings 24 and 26—28 gave 53 birds with extra toe on both sides.

* This egg was opened at the 14th day, and as the condition could not be clearly made out, it is entered as intermediate. Probably, if it had been reared, it would have been an r.c. The same applies to the "doubtful" in Experiment 18.

Taken together there were—

R.c.	Interm.	S.c.	E.t. both sides.	E.t. one side.	No e.t.
123	1	1	100	5	2

The dominance of the rose comb is therefore almost complete, while that of the extra toe, though very strong, is not quite so complete. Experiment 25 proves that the dominance of the extra toe was distinctly imperfect as against the normal foot of the Brown Leghorn ♂. These results are referred to on p. 113.

White Wyandotte and White Leghorns.

		R.c.	S.c.
30.	Wy. ♀ (1 year) × Legh. Babr. ♂ (1 year)	17	0
31.	„ (2 years) × „ LK ♂ (3 years)	5	0
32.	„ (1 year) × „ 40 ♂ (1 year)	3	0
33.	„ (2 years) × „ 91 ♂ (1 year).........	20	0

In all, therefore, this hen produced 45 rose combed chicks by four cocks and no single comb.* All the chicks reared were white, or white with a few ticks of black, barred in several. The general shape agreed nearly with the Wyandotte: legs and bill yellow, ear-lobes red patched with white.

Experiments 1—33, therefore, show that the pea comb, rose comb, and extra toe are in certain strains dominant almost without exception. A distinct departure from this regular dominance as regards toe is seen in Experiment 25 (see p. 113).

First Crosses bred together.

34. From Experiment 17, Brown Leghorn 1 ♀, by Indian Game 59 ♂, 4 pullets and 1 cockerel were taken, and their eggs incubated through the whole breeding season of 1901.

They gave 166 pea combs and 59 single-combs, or 2·8 : 1. All the chicks were more or less dark on hatching. Those that were lightest were buff but had dark quills showing, so that there is no doubt they would all have proved dark birds.

35. The cock (dark; pea comb) used in Experiment 34 was put with 5 hens (light; pea comb), viz., 3 that had been used in Experiment 36, 1 bred in Experiment 14, and 1 bred in Experiment 5. This was at the end of the season, 1901, when most hens had stopped laying. It was not known which hens laid the eggs, but they gave collectively 19 p.c. and 6 s.c., or 3·1 : 1.

The colour-result was altogether *contrary* to simple expectation on the hypothesis that the colorations of Brown Leghorn and Indian Game can be treated as both alike "dark." The chicks were nineteen dark and six light, whereas equality would be expected on the above hypothesis. [See note, p. 141.]

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* Mr. Grosvenor Berry informs us that in crosses he has made with Golden Wyandotte, the rose comb was always dominant, without exception, over single comb.

36. From Experiment 17 (Leghorn Babr. 42 ♀ × Indian Game 59 ♂) four pullets and one cockerel were similarly bred together for the season, 1901, with the result 147 pea comb, and 45 single comb, or 3·27 : 1.

In this case the grandparents were of strikingly different colours, white and dark respectively, and as has been said the first crosses in these matings are light birds. Taken broadly, therefore, *light* is here dominant, and dark is recessive, and, as a matter of fact, the offspring of Experiment 36 consisted of 149 light, and 41 dark, or 3·6 : 1, a proportion not greatly removed from 3 : 1.

Grouped according to both characters, comb and colour, the offspring were—

Light with pea comb	111
,, single comb	37
Dark with pea comb	34
,, single comb..................	8

If the numbers followed strictly Mendel's law, they should be a 9 : 3 : 3 : 1.

It must be remembered that here the terms "light" and "dark" each cover several different conditions of plumage, and to this question we shall return, only noting here that adopting this grouping the Mendelian proportions are not very widely departed from (*cf.* p. 109).

37. From Experiment 29, 2 pullets and 1 cockerel were taken and bred together through 1901. They gave 70 rose combs and 13 single combs. These numbers depart very widely from 3 : 1, being in fact, 5·4 : 1. As regards foot they gave 61 chicks with both extra toes, 2 with only 1 extra toe, 22 with no extra toe, thus giving 2·9 : 1. (As to these numbers, see note, p. 140.)

Grouped according to both characters they gave—

R.c. with e.t. (including halves)......	50
R.c. without e.t.	19
S.c. with e.t.	10
S.c. without e.t.	3

There again the numbers should follow 9 : 3 : 3 : 1, from which they considerably depart, owing to the deficiency of recessive combs. We may note that the Mendelian series most nearly fitting these figures are 45 : 15 : 15 : 5.

38. Three pullets and a cockerel from Experiment 24 bred together to end of March, 1901, gave, as regards comb, 85 r.c. and 17 s.c., and as regards toe, 77 with both extra toes, 1 with one extra toe, 29 with

no extra toe. Here also the combs depart widely from 3 : 1, being 5 : 1 (*cf.* Experiment 37), while the toes being 78 : 29, agree precisely, being 3·0 : 1. (As to these numbers, see note, p. 140.)

Grouped according to both characters, they were—

R.c. with e.t.	64
R.c. without e.t.	21
S.c. with e.t.	12
S.c. without e.t.	5

The nearest Mendelian series of numbers is 63 : 21 : 21 : 7.

In this experiment six *dark* chicks (not reared) occurred, though both birds in Experiment 24 were light (see p. 98).

39. At the end of March the cockerel used in Experiment 38 died of tuberculosis, and the cockerel used in Experiment 37 was put to the hens of Experiment 38. On reference to Experiments 24 and 29, it will be seen that the cock was in composition the reciprocal of the hens. As the results of the two experiments were similar, the hens were put to the new cock without an interval, and consequently a few of the chicks here reckoned were doubtless by the first father. At the end of the season also the hens of Experiment 37 were added to those of Experiment 38, and laid about 10 of the chicks here reckoned.

The results were 118 rose combs, 35 single combs; 131 with both extra toes, 28 with no extra toes. The combs are therefore in the ratio 3·3 : 1 and the feet 4·7 : 1.

Grouped according to both characters, there were—

R.c. with e.t.	94
R.c. without e.t.	23
S.c. with e.t.	32
S.c. without e.t.	3

Here there is a considerable deficiency of no e.t. birds. The nearest Mendelian series is 90 : 30 : 30 : 10.

No dark chicks occurred here.

Experiments 37, 38 and 39 together give—

R.c., 273; s.c., 65; or 4·2 : 1
E.t., 272; no e.t., 79; or 3·4 : 1

Grouped according to both characters—

R.c. with e.t.	208
R.c. without e.t.	63
S.c. with e.t.	54
S.c. without e.t.	11
	336

As was seen in Experiments 37 and 38, the recessive *combs* were deficient, while in Experiment 39 the greater deficiency was in the recessive *feet*. These two deficiencies in this final table partly cancel each other, but as the whole number in Experiment 39 was far greater than in the other two, the table is overweighted by the peculiarity of that family.

In the chief departures from 3 : 1, the near approaches to 5 : 1 should be noticed, viz. :—

In Experiment 37 the combs are ...... 5·4 : 1
,, 38 ,, ,, ... 5·0 : 1
,, 39 the feet are .... 4·7 : 1

Whether this is a mere coincidence without further significance cannot yet be said.

Wyandotte-Leghorn First Crosses bred together.

40. Four pullets and one cockerel from Experiment 33 bred together until end of July, 1901, gave 196 rose combs and 79 singles, which is approximately only 2·5 : 1. Here the *recessives* for the first time considerably exceed the expected proportion of 1 : 3.

It is a remarkable fact that in this mating a number of *dark* chicks were produced, the numbers being 215 light and 55 dark. But the Wyandotte grandmother, though a white bird without ticks, may for anything known to the contrary have been a cross between a dark and a white bird. If so, her offspring by a White Leghorn, taking white as dominant, would all be light, though consisting of DD and DR birds in equal proportions. It would thus be an even chance that any of the birds used in Experiment 40 were DD or DR. The cock is in any case DR (on this hypothesis). If then one of the hens were DD and the other three DR, the ratio 13D : 3R would be expected, which approaches fairly nearly to 215 : 55. This of course is a mere suggestion; otherwise unsupported.

Several of the results obtained in the foregoing experiments depart considerably from the Mendelian expectations. It is, however, to be remembered that these expectations give average results only. In all cases yet investigated, individuals differ greatly in the results they give, and we can only suppose that these differences represent different proportions in the number of effective dominant and recessive germs which they produce. By putting more than one female in each experiment, we may suppose that cancelling has occurred as betwen the female peculiarities, but as only one male was used at a time, his peculiarities have full scope. For example, the following experiment goes some way towards showing that the aberration of the comb-numbers may be due to this cause.

Dominant First Crosses bred with Pure Recessive.

41. The four pullets used in Experiment 40 after their resting-season were for the remainder of 1901 put with a pure Leghorn cockerel Leg. 369 ♂. They gave 46 r.c. and 50 s.c., or almost equality, which the law demands. All chicks of course light in colour. This experiment was very kindly carried out for me by Mr. R. Assheton, Lecturer on Biology to Guy's Hospital.

42. A similar experiment was made with three dominant first crosses raised respectively in Experiments 5, 15, and 16. Put with a pure Leghorn (355 ♂), for the latter weeks of 1901 they gave—

P.c.	S.c.	Light down.	Dark down.
28	30	57	0

Here again the approach to equality is very close. There are of course no dark coloured chicks, as only one grandparent was coloured.

Nevertheless, that the peculiarity of the male if permanent is not of itself enough to explain the aberrations, is shown by a comparison of Experiments 37 with 38 and 39. In Experiment 37 the same male was used as in Experiment 39, the females being the same in Experiments 38 and 39. But while the feet are practically 3D : 1R in Experiments 37 and 38, they are 4·7 : 1 in Experiment 39. Conversely, while the combs are 3·3 : 1 in Experiment 39, they are about 5 : 1 in the other two experiments. There is at present no obvious explanation of these results, and we can only accept the conclusion that not only different individuals similarly bred may give different proportions, but that these proportions may change also at different times (*cf.*, p. 121).

TOTALS OF MENDELIAN FIRST CROSSES BRED TOGETHER.

Experiments 34—39, added together, give the following totals. Though not strictly legitimate, such promiscuous addition is rendered less objectionable for the reason that in the case of each character which departs considerably from 3 : 1, there are grounds for regarding such a departure as an oscillation and not a departure peculiar to the character.

Pea comb and single comb—

	P.c.	S.c.
Experiment 34............	166	59
„ 35............	19	6
„ 36............	147	45
	332	110 or 3 : 1

Dorking rose comb and single comb—

	R.c.	S.c.
Experiment 37...........	70	13
" 38...........	85	17
" 39...........	118	35
	273	65 or 4·2 : 1

Wyandotte rose comb and single comb—

	R.c.	S.c.
Experiment 40...........	196	79 or 2·5 : 1

Dominant combs together 801, and recessives 254, or 3·1 : 1.

Extra toe and no extra toe—

	E.t.	No e.t.
Experiment 37...........	63	22
" 38...........	78	29
" 39...........	131	28
	272	79 or 3·4 : 1

Taking combs and feet together there are 1073 : 333, or 3·2 : 1.

Colours.

Plumage.—The case of plumage is a much more complex one, and it is very doubtful if the results on this head should be added to the others at all. As was stated above, first crosses are white, or nearly white, birds. We may therefore regard "light" as dominant against "dark." Moreover, as the colours were in most cases judged on very young chicks, they can only be taken as an indication of down-plumage. But from those that were reared to maturity, it is certain that the "dark" class consists of a number of different kinds of colours, some of which are recurrent and definite, while others are irregular mixtures. At the present time statistics as to these types of coloration cannot be given, though probably another season's work may supply them. An outline of the probable significance of such a series of colorations produced by the first crosses interbred is given under the head of "Compound Allelomorphism." Among the "dark" types produced by the Brown Leghorn-White Dorking first crosses interbred (Experiment 81), were a black form, a cuckoo form, a form like Brown Leghorn spotted with white, female birds of the colour proper to Silver-greys and Duckwings, *i.e.*, white hackle striped with black, grey mottled wings and mantle, with chestnut breast (corresponding male not hitherto seen).

In the "dark" class the Indian Game-White Leghorns (Experiments 36 and 76—80) gave some blacks, some cuckoos, and some nearly approaching Indian Game.

In each case the "light" classes consist of some pure white birds, many white birds flecked with black or red, such as occur in the first crosses; and in the Br. Legh.-Dorking crosses, some white birds with chestnut breasts ("pile").

Until the experiment is completed, no statement can be made, but the opinion may be hazarded that at least some of these colour forms, if corresponding cocks and hens were mated, would breed true from their first appearance (see p. 144).

The Experiments 76—81, from which the colour results are now under discussion, were made with families which were non-Mendelian as regards structural characters, but as regards colour these families were Mendelian in the sense that "light" was dominant against "dark."

Remembering the *caveat* expressed above, taking all cases in which the first crosses between dark and white breeds have been bred together, we have the following results :—

	Light down.	Dark down.
Experiment 36	149	41
,, 76	50	10
,, 77	49	16
,, 78	56	24
,, 79	106	40
,, 80	8	1
,, 81	131	44
	549	176 or 3·1 : 1

Grand Totals.

Adding all dominants and all recessives, we have—

	Dom.	Rec.
Pea comb and single	332	110
Dorking rose comb and single	273	65
Wyandotte rose comb and single	196	79
Extra toe and no extra toe	272	79
Light down and dark down	549	176
	1622	509 or 3·18 : 1

Though this total agrees closely with the expected 3 : 1, it must not be forgotten that several of the observations which contribute to the result show considerable departures from it, and we may suspect that some of these are not merely fortuitous accidents.

For the present also, we do not know that the extracted recessives are pure, or that the dominants consist of pure and crossed, as they may be expected to do, in the proportions of 1 : 2. But taken generally, there is so close an agreement with expectation that these propositions on which the expectation is based, can scarcely be other than at least a fair approximation to the truth.

Colour of Legs.

The colour of legs and bills cannot be safely determined till maturity, and consequently the numbers are too small to warrant a statement of statistical proportions. It may nevertheless be stated that *qualitatively* the offspring of first crosses between White Dorking and the Leghorns agree with the Mendelian expectation. As stated above, such first crosses have whitish legs, but the offspring of the first crosses bred *inter se* have *either* white (including whitish) legs *or* yellow legs.

General Result.

Taking together the structural characters of comb and foot and the colour of legs it appears that each is transmitted independently. As a result, therefore, the several characters may be combined in individuals bred from first crosses *inter se* in any combination, producing, for example, birds with single comb, extra toes and white legs; rose comb, no extra toe and yellow legs, &c., thus fulfilling the Mendelian expectation, though how far the ratios of each combination agrees with that principle, the observations are insufficient to determine.

NON-MENDELIAN GROUP.

We have next to consider a more complex series of results. It has now been shown that in the case of a considerable number of Indian Game, the pea comb is an almost exclusively dominant character as against single comb. Similarly in three White Dorkings the rose comb proved to be a dominant character, and in two of these birds the extra toe was also dominant. In the cases now to be described there was no exclusive dominance, but on the contrary the offspring was always *mixed*, some being pea and some single in the Indian Game crosses, and some rose and some single in the Dorking crosses.

Indian Game and Leghorns giving Mixed Offspring in First Crosses.

In the list of original Indian Game birds there are (1) five closely bred birds of one strain (p. 90, 1 and 2); (2) two hens (p. 91, 3) by a cock of the same strain as (1) out of a hen remotely related. All these birds showed dominance, which was practically exclusive. Of the two birds named in 4 (p. 91) the hen, Brom. ♀, was shown to be exclusively dominant with one Leghorn cock, and the same is the case with regard to the cock Rd. ♂ in 5 (p. 91).

On the contrary, the cock in 4 (p. 91) Brom. ♂ and the cock in 6 (p. 91), Gr. ♂, gave mixed offspring with Leghorn hens, as follows :—

		P.c.	S.c.
43.	Legh. LK ♀ (1 year) × I.G. Brom. ♂ (1 year)	7	18
44.	,, Babr. 42 ♀ (1 year) × I.G. Brom. ♂ (2 years)	10	10
45.	,, Rd. ♀ (1 year) × I.G. Brom. ♂ (2 years) ...	7	5
46.	,, 47 ♀ (1 year) × I.G. Gr. ♂ (1 year)........	14	21
47.	,, 47 ♀ (2 years) and 89 ♀ (3 years) } × I.G. Gr. ♀ (2 years).	15	8
	Of these 5 p.c. and 3 s.c. were laid by 89 ♀ alone after removal of 47 ♀.		
48.	Legh. ♀ (breeding unknown) × I.G. Gr. ♂ (1 year)	8	4
	This hen was used in Experiment 8 (*q.v.*).		

Each mating therefore in which these cocks were used, resulted in a mixture of pea and single, though the proportions vary greatly.

A family (see table, p. 112) of five Indian Game birds were raised from the hen BLR ♀ and Brom. ♂. Of these, three were females, viz., I.G. 17 ♀, I.G. 90 ♀, and I.G. 94 ♀, and two were males, I.G. 12 ♂ and I.G. 15 ♂. Bred with Leghorns these five birds gave mixtures as follows :—

		P.c.	S.c.
49.	I.G. 17 ♀ (1 year) × Babr. ♂ (1 year)	20	16
50.	,, (2 years) × Legh. 285 ♂ (1 year)	16	14
51.	,, (3 years) × Legh. 673 ♂ (1 year)	12	11
52.	I.G. 94 ♀ (1 year) × Legh. 40 ♂ (1 year)	2	8
53.	,, (2 years) × Legh. LK ♂ (2 years)......	15	10
54.	,, (2 years) × Legh. 91 ♂ (1 year)........	9	16
55.	,, (3 years) × Legh. 91 ♂ (2 years).......	4	1
56.	I.G. 90 ♀ (2 years) × ,, (1 year)	6	12
57.	,, (3 years) × ,, (2 years)	6	2
58.	,, (2 years) × Legh. 285 ♂ (1 year)	5	3
59.	,, (3 years) × Brown Legh. ♂ (2 years)...	13	11
60.	Legh. Babr. 89 ♀ (2 years) × I.G. 15 ♂ (2 years)..	8	5
61.	Legh. Babr. 110 ♀ (1 year) × ,, (1 year) ..	12	12
62.	Brown Legh. ♀ Br. L. 1 (1 year) × I.G. 12 ♂ (1 year)	4	8

It is seen, therefore, that each of three hens and two cocks, raised as above, gave mixtures when bred with various Leghorns, and again the proportions of such mixtures vary greatly. Two of these I.G birds, out of BSR ♀ × Brom. ♂, viz., I.G. 90 ♀ and I.G. 12 ♂, were selected, and from them were raised a family of which two only survived. This family consisted of *six chicks with single combs* (see p. 112) and six with pea combs, among which were the two survivors, I.G. 59 ♂ and 120 ♀. The supposed "pure" I.G. birds, therefore, themselves gave a mixture; but the only two survivors, themselves pea-combed, gave exclusively pea-combed offspring, with one doubtful exception only (see Experiments 15—19A).

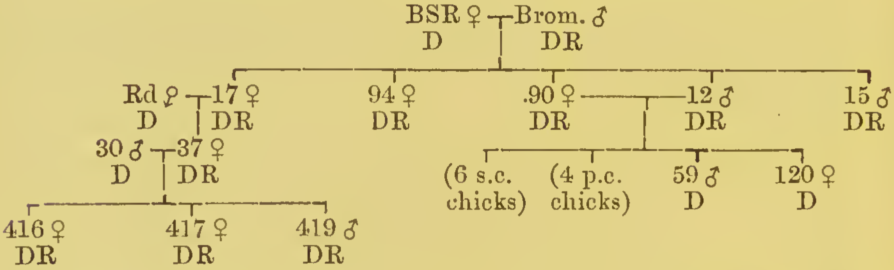
From I.G. 17 ♀ × I.G. Rd. ♂ was produced a family of thirteen chicks, all pea comb. Of these, one, I.G. 37 ♀, was crossed with a Leghorn ♂ as follows:—

		P.c.	S.c.
63.	I.G. 37 ♀ (2 years) × Legh. 373 ♂ (1 year)........	28	29

Previous to the foregoing crosses, I.G. 37 ♀ was bred with I.G. 30 ♂, producing a series of chicks all pea combed, of which two pullets, I.G. 416 ♀ and 417 ♀, and one cockerel I.G. 419 ♂, have been crossed with Leghorns as follows:—

		P.c.	S.c.
64.	Legh. 47 ♀ (2 years) × I.G. 419 ♂ (1 year).......	4	4
65.	„ 96 ♀ (2 years) × „ (1 year).......	11	14
66.	„ 114 ♀ (1 year) × „ (1 year).......	2	5
67.	„ 372 ♀ (1 year) × „ (1 year).......	7	10
68.	I.G. 416 ♀ (1 year) × Legh. 91 ♂ (2 years)......	3	8
69.	„ 417 ♀ (1 year) × „ 369 ♂ (1 year)......	6	4

Table of Relationship of I.G. Birds which gave Mixtures.



In the above table all those that were tested and found to give no mixtures are labelled D, while those that gave mixtures are labelled DR. As stated in the text, 90 ♀ × 12 ♂, though supposed thoroughbreds, gave a mixture of 6 s.c. and 6 p.c. when bred together. The labelling D and DR is put in to show how far what is called hereafter (p. 117) the "First Hypothesis" agrees with the facts.

On the contrary, it must be noticed that all the nine "out-bred" birds gave mixtures as expected on the "Second Hypothesis" (p. 119).

White Dorkings and Leghorns giving Mixed Offspring in First Crosses.

As stated in Experiments 24—29 (p. 102) the three birds from the Cresswell strain showed practically complete dominance of the rose comb (59 r.c., 1 s.c.). As regards foot, all these six matings showed the extra toe dominant except one (Experiment 25), in which two chicks had no extra toe and four had an extra toe on one side only.*

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* As mentioned (p. 98), the mother of these chicks, Cr. 121 ♀, showed a secondary tinged with buff on the second moult, and it is not doubtful that the White Dorking is remotely connected with the coloured Dorking. This sign of impurity might be supposed to show impurity in comb, inasmuch as the Coloured or "Dark" Dorking is usually s.c., but its foot of course has the extra toes of the Dorkings.

Of the two birds, ♂ and ♀, from Miss Knowles, the cock only was tried with Leghorns. In each case he gave some recessives, both as regards comb and toe, as follows :—

70. Legh. Babr. 42 ♀ (2 years) × Dork. K. ♂ (1 year) gave in 1900—

R.c.	S.c.	Both e.ts.	1 e.t.	No e.t.
30	18	46	1	1

71. Legh. Babr. 42 ♀ (3 years) with Legh. Babr. 110 ♀ (3 years) } × Dork. K. ♂ (2 years) gave in 1901—

R.c.	S.c.	Both e.ts.	1 e.t.	No e.t.
31	21	64	1	2

72. Legh. Babr. 42 ♀ (3 years) alone × Dork. K. ♂ (2 years) gave in 1901—

R.c.	S.c.	Both e.ts.	1 e.t.	No e.t.
29	19	36	1	0

73. Legh. Babr. 110 ♀ (3 years) alone × Dork. K. ♂ (2 years) gave in 1901—

R.c.	S.c.	Both e.ts.
8	7	15

74. Brown Legh. Br. L. 1 ♀ (2 years) × Dork. K. ♂ (1 year) gave in 1900—

R.c.	S.c.	Both e.ts.	1 e.t.	No e.t.
35	36	59	7	5

75. Br. L. 1 and Br. L. 2 together (3 years) × Dork. K. ♂ (2 years) gave in 1901—

R.c.	S.c.	Both e.ts.	1 e.t.	No e.t.
57	68	93	17	16

Between these two hens the last results cannot be allotted with certainty, but it was known that Br. L. 1 ♀ contributed to these totals at the end of the season after removal of Br. L. 2 ♀.

R.c.	S.c.	Both e.ts.	1 e.t.	No e.t.
25	28	46	3	5

25. In regard to *comb* this experiment has been given in the Mendelian group, for the r.c. showed full dominance so far as the numbers went. As regards foot-character the case belongs here.

Cr. ♀ 121 (2 years) × Brown Legh. ♂ (2 years) gave—

R.c.	S.c.	Both e.ts.	1 e.t.	No e.t.
22	0	16	4	2

It is to be remembered that the hen belonged to the strain of White Dorkings which, with other Leghorns, showed dominance of extra toe.

76. Legh. 378 ♀ (1 year) × Dork. K. ♂ (2 years) gave—

R.c.	S.c.	Both e.ts.
2	5	8

These birds were only together for a fortnight at the end of the season.

As told on p. 93, from Miss Knowles's two birds, which may or may not have been nearly related—were bred two pullets, Dorkings 262 ♀ and 263 ♀, and one cock, Dorking 258 ♂, which gave following results. Both pullets were exceedingly sterile. They were hatched on May 22 of the previous year, and so can hardly be considered very "late hatched."

77. Legh. 378 ♀ (1 year) × Dork. 258 ♂ (1 year) gave—

R.c.	S.c.	Both e.ts.	No e.t.
19	36	55	0

78. Dork. 262 ♀ (1 year) × Legh. 91 ♂ (2 years) gave—

R.c.	S.c.	Both e.ts.
1	1	2

79. Dork. 263 ♀ (1 year) × Legh. 373 ♂ (1 year) gave—

R.c.	S.c.	Both e.ts.
4	0	4

Matings with Members of Mixed First-cross Families.

A. *From Indian Game and Leghorns.*

Three first-cross pullets 111 ♀ and 151 ♀, both pea-comb birds, and 149 ♀, a single-comb bird, were bred with their own brother, 112 ♂ (all raised in Experiment 58), for the whole season 1901. These four birds were all white, ticked.

80. Cross-bred 111 ♀ p.c. (1 year) × cross-bred 112 ♂ p.c. (1 year) gave—

P.c.	S.c.	Lt.	Dk.
38	22	50	10

81. Cross-bred 151 ♀ p.c. (1 year) × cross-bred 112 ♂ p.c. (1 year) gave—

P.c.	S.c.	Lt.	Dk.
46	21	49	16

82. Cross-bred 149 ♀ s.c. (1 year) × cross-bred 112 ♂ p.c. (1 year) gave—

P.c.	S.c.	Lt.	Dk.
34	50	56	24

83. Three s.c. pullets, first crosses, cross-bred, ♀'s 44, 71, 117 (1 year), raised in Experiment 50, were bred for most of the season with a single comb cross-bred 97 ♂ (1 year) raised in Experiment 54. All four were white ticked birds. They gave—

P.c.	S.c.	Lt. down.	Dk. down.
0	149	106	40

These four birds with recessive combs therefore produced no dominant comb at all.

84. A pea comb cross-bred 77 ♀ (1 year) raised in Experiment 54 with the same cockerel as used in Experiment 83, for a few days only gave—

P.c.	S.c.	Lt. down.	Dk. down.
6	3	8	1

B. *From White Dorkings and Leghorns.*

85. Two r.c., e.t. pullets, cross-bred, 249 ♀ and 278 ♀, raised in Experiment 74 (out of Brown Leghorn 1 ♀ × Dorking K ♂), bred for the season 1901 with own r.c., e.t., brother gave—

R.c.	S.c.	Both e.ts.	1 e.t.	No e.t.	Lt. down.	Dk. down.
131	53	135	8	49	131	44

86. A pullet, s.c., e.t., cross-bred, 317 ♀, raised in Experiment 70, was bred till end of May, 1901, with cockerel s.c., *no* e.t., cross-bred, 305 , raised in Experiment 74, gave—

R.c.	S.c.	Both e.ts.	1 e.t.	No e.t.	Lt. down.	Dk. down.
0	60	45	1	14	60	0

In this experiment again, the birds with recessive combs have been unable to produce any dominant comb. On the other hand, the fact that the cockerel was without extra toes does not seem to have had any effect on the proportion of e.t. to no e.t., which are approximately 3 : 1, as would have been expected if the parents had been dominant first crosses from a Mendelian family. These birds had only one coloured grandparent, and are therefore unable to produce any dark-coloured offspring, in conformity to the expectation.

87. A pullet, own sister to those used in Experiment 86 (raised in Experiment 70), but *rose* combed, with extra toes, by the same ♂ 305, s.c., *no* e.t., gave—

R.c.	S.c.	Both e.ts.	No e.t.	Lt. down.	Dk. down.
8	7	10	5	15	0

88. The same cockerel, cross-bred 305 ♂, used in Experiments 86 and 87, was put for the latter weeks of the season 1901 with six

pure Leghorn hens of various ages, and breeding. They collectively gave—

R.c.	S.c.	Both e.ts.	1 e.t.	No e.t.
0	152	77	1	78

138 are recorded as light chicks, and there were none dark.

Here again the cockerel, *without extra toes*, gives the same result as if he had been a Mendelian dominant first cross! The absence of dark-coloured chicks is, of course, to be expected, as only one grandparent was coloured.

Discussion of Non-Mendelian Group.

It has been seen that in the crosses both of Indian Game with Leghorns, and of Dorkings with Leghorns, the results divide themselves into two groups. In the first group the first crosses, almost without exception, exhibit the dominant characters, and the subsequent progeny produced by breeding these first crosses *inter se* obey Mendel's Law fairly well. There are departures from the law which may possibly indicate special disturbing causes, but the general applicability of the principle is unmistakable.

The second or non-Mendelian group of cases is much more obscure, and their significance is quite different as they are regarded in one of two ways. The question on which the whole difficulty turns may be then expressed: Can birds, which themselves exhibit dominant characters, even on crossing with recessive birds, produce recessive offspring *if they would not have produced recessive offspring when bred* inter se? Otherwise, though less correctly, the question may be expressed thus: Is the fact that certain supposed pure dominants gave some recessives when crossed with recessives, to be ascribed solely to the fact that the dominants were impure? "Pure" and "impure" are not here used quite in the ordinary sense of the fancier. "Pure" means producing gametes which all transmit the same character and are homogeneous; "impure" means producing gametes of more than one kind, heterogeneous in regard to the characters they bear. Simple purity of descent is not in question,* for as we now know, the "purity" required may be the attribute of any individual of the form DD or RR, though of immediately mixed descent. In Mendelian terms, does DR ever appear recessive in these cases, or does such a recessive appearance always indicate that the individual is really RR? Unfortunately the material for finally answering this question in the case of the *combs* is not before us. It was not until the bearing of the Mendelian discovery was fully realised, and its applicability to these phenomena shown, that the absolute necessity for a decision on this point became evident. Moreover, until at the very least three successive generations have been bred the point cannot be quite decided. We may then usefully at this stage consider the facts briefly in the light of each of these two hypotheses, and point out how far either of these suppositions is consistent with observation.

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* Inquiry as to whether recessives had ever occurred in the yards from which the birds in question came elicited that in the case of I.G. Brom. ♂ the question could not be answered. In the case of the Dorking, Miss Knowles very kindly writes that an occasional single comb is seen from time to time, perhaps about 1 in 30, and also an occasional four-toed bird; but that the number of such recessives is much greater when fresh blood is introduced.

First Hypothesis: that every Recessive is, in composition, RR.

According to this view the two original Brom. birds must be regarded as of different composition, the ♀ giving × Leghorn LK ♂ (Experiment 20), 18 p.c. and 0 s.c. is probably to be considered as pure dominant, DD. The ♂, however, gave by three different Leghorn hens in

	P.c.	S.c.
Experiment 43	7	18
„ 44	10	10
„ 45	7	5

He would therefore be regarded as a dominant cross, DR. We note that in Experiment 43 the numbers 7 : 18 are far from the expected 1 : 1, being 1 : 2·5. To this point reference will again be made.

The same ♂, whose possible "impurity" was then unsuspected, bred (see table, p. 112) with I.G. BSR ♀ of undoubted "purity," gave five birds, of course all p.c. We expect, then, that of these half were DD and half DR. But *all* these five I.G.'s, when crossed with Leghorns, gave mixtures, as told in Experiments 45—58, the proportion of p.c. to s.c. being again very various, though, as a matter of fact, the totals, 122 p.c., 113 s.c., approach the expected equality. Five is a small number for such a test, still it is noticeable that *none* of them appeared to be DD, while on this hypothesis *half* should have been so.

Of these five birds two were bred together, and, as told on p. 112, there was at once a mixture of peas and singles, 6 p.c., 6 s.c., the hypothesis expecting 3 p.c. : 1 s.c. Of these birds, unfortunately, two only, both p.cs., survived to be tested. *Both were pure dominants DD*, though DD : DR should here be 1 : 2.

One of the five birds (I.G. ♀ 17) here assumed to be DR. with three Leghorn ♂'s gave 48 p.c. and 41 s.c. (Experiments 49—51) closely approaching the expected equality.

This hen was bred with I.G. Rd. ♂. As to the latter the evidence is that he gave (Experiment 21) with a Leghorn ♀ 29 p.c. and 1 s.c., which is a close approximation to purity. With I. G. ♀ 17 he gave a family, all p.cs., of which one alone was tested, I. G. ♀ 37, proving (Experiment 63) to be, on the hypothesis, DR, and giving × Leghorns

373 ♂, 28 p.c. 29 s.c., or the expected 1 : 1. The same hen × I.G. 30 ♂, of established purity (Experiments 5—8), gave a family of Indian Games, all p.c. of course. Three of these were tested (Experiments 64—69), giving in each case a mixture, the proportions again varying.

In addition, therefore, to the five birds reared out of BSR ♀ × Brom. ♀, we have one bird out of I.G. 17 ♀ × Rd. ♂, and three birds out of I.G. 37 ♀ × I.G. 30 ♂, nine birds in all, which gave mixtures on crossing with Leghorns, and *none* which did not give mixtures, though the hypothesis expects that *half* of them would give such mixtures, and that *half* would not. This discrepancy, though far from amounting to proof, nevertheless gives a decided suggestion that the hypothesis we are considering is insufficient to thoroughly explain the phenomena. It must be noticed, too, that all the nine supposed DR birds were *out-bred.*

Taking now the Dorking cases, it is clear that as regards comb the Cresswell strain comes very near "purity," giving, on crossing with Leghorns (Experiments 24—29), 123 r.c., 1 s.c., 1 intermediate.

As regards extra toe, we have already called attention to the fact that as Experiment 25 shows, the evidence is not quite so absolute.

The Knowles strain was represented by two birds, K ♂ and K ♀. The male gave, on crossing with Leghorns, mixtures both as regards comb and toe (Experiments 70—76). The female, now dead, was never tested by crossing.

As the offspring of these two there are three birds of which two gave mixtures of combs on crossing (Experiments 77—79), and the third was insufficiently tested. So far, however, there is no mixture in regard to foot.

Finally, we have to consider the unexpected facts shown by Experiments 83, 86, and 88, in which it appeared that cross-bred birds (both Dorking—Leghorns and Indian Game—Leghorns alike) with recessive combs, whether bred together or with pure recessives, gave *only recessives* so far without exception. (Also in Experiment 82 a recessive cross-bred with a dominant own brother gave a considerable excess of recessives, viz., 34 p.c. and 50 s.c.)

Now if the hypothesis we are considering be the true one, this fact becomes explicable; for in the cases where a mixture occurs on the first cross, we should thus expect that any recessive produced would be pure. This fact is so remarkable and so difficult of explanation on any other supposition that it may naturally be thought to outweigh all other discrepancies.

But this simple explanation is not applicable to the case of extra toe. There is so far the evidence of only one bird—the cross-bred 305 ♂. This bird, which had single comb and *no trace whatever of* *extra toe*, nevertheless when bred with pure Leghorn hens gave as many chicks with extra toes as without them (Experiment 88). As regards foot, therefore, this cross-bred recessive was not only not pure, but behaved exactly like a cross-bred dominant. Such a fact must be a complete refutation of the hypothesis of "impurity" as a sufficient explanation of the occurrence of recessive foot in the first crosses.

It also suggests very strongly that in cases where neither character has complete dominance, the first cross may produce equal numbers of gametes transmitting each character, just as in strictly Mendelian cases, a point on which more evidence is greatly needed. In such a case selection among the first crosses may effect nothing.

Second Hypothesis: that Recessives produced on the First Cross may be of the Composition DR, the usually dominant Character having Receded.

That this hypothesis is a true one in the case of the extra toe is certain, as stated in the last paragraph. If, then, a character, usually recessive, may thus dominate in the first cross, it may become necessary to regard as crosses some of the recessives produced by cross-bred dominants bred *inter se*, and very serious complexity may thus attend the unravelling of breeding results, though the transmission of character may occur in the strictly Mendelian method by pure gametes.

Seeing that this may certainly be so in the case of feet, we have to consider how the facts stand in regard to comb.

A preliminary consideration which goes against the view that both the Brom. and K. birds were merely impure, in the ordinary sense of being sensibly mongrelised with some other breed, is the fact that none of the birds bred thus far show any unexpected character except in regard to comb. In other characters, notably the brown colour, a character especially complex and likely to show such impurity—there is no noticeable departure from the respective breeds.*

On the hypothesis now before us the question arises, Why is it that some birds should have given mixtures on crossing while others did not? Also, Why do some birds on crossing give mixtures in such different proportions? Until the facts were examined in the light of Mendel's discovery, it was proposed to answer these questions by reference to the suggested effect of *in-breeding*. The B.S. strain had been long in-bred, and the fact that on crossing they gave no mixture was attributed to this cause. On *out-breeding* this strain with Brom. ♂ (see table, p. 112), birds were produced which gave *mixtures* on crossing. On breeding two of these out-bred birds together, brother and sister, two birds, I.G. ♂ 59 and ♀ 120, were produced which were *wholly dominant*, again, as was supposed on account of the close breeding.

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* Beyond the occasional appearance of white feathers in the wing quills.

On again out-breeding the out-breds with I.G. Rd. ♂, the hen I.G. ♀ 37 was produced, which again gave mixtures. This hen by the in-bred ♂ 30, a pure dominant, gave again three birds, 416 ♀, 417 ♀, and 419 ♂, which all produced mixtures on crossing. This last fact was attributed to the circumstance that the mother, I.G. ♀ 37, was thoroughly out-bred. Thus *all* nine birds which gave mixtures, lettered DR in table (p. 112), were out-bred.

Again the Cresswell strain of Dorkings, which was stated to be closely bred, was found to show pronounced dominance. The Knowles strain on the contrary was almost certainly not much in-bred, and the only bird tested was found to give a mixture on crossing.

This is again noticeable in the experiments made with the Dorking ♂ K. Bred wfth two in-bred Brown Leghorn hens through two seasons (Experiments 74 and 75) the singles were in a slight excess, the numbers being in all 92 r.c., 104 s.c., while the same cock with two White Leghorns, not in-bred, gave 98 r.c., 65 s.c., or roughly 3 : 2, the excess being on the r.c. side (Experiments 70—73).

As regards foot, the evidence points in the same direction, the White Leghorns scarcely producing any birds without extra toes, though the in-bred Brown Leghorns produced about 10 per cent. Evidence of the same kind was seen in Experiment 25 when the male Brown Leghorn was used.

Thus after the first three years, when it had been found that the males, Leghorns 40 ♂ and 91 ♂ (Experiments 52, 54, and 56), gave a distinct excess of singles over pea combs, and that the in-bred Brown Leghorn 1 ♀ gave a greater proportion of rose combs than out-bred hens did with the same cock, the evidence taken with the obvious dominance of the in-bred B.S. Indian Games and the Cresswell Dorkings seemed to show that in-breeding had the suggested effect.

Reference, however, to the preserved dead chicks out of LK ♀ × I.G. Brom. ♂ (Experiment 43) previously misunderstood* showed that the numbers were as stated, seven pea comb and eighteen single comb. The mother, therefore, of 91 ♂, though herself not in-bred, gave an even greater excess of singles than 91 ♂, which was certainly *somewhat* in-bred.

It must also not be forgotten that even the most decided dominants did as a rare exception give an occasional recessive on crossing with pure recessive (see Experiments 13, 21, 22, 22*a*), so that the possibility is established that in birds which are unquestionably DR by breeding, the recessive comb *may* appear.†

To sum up: for the considerations already given, there is no *certain* evidence that in-breeding has increased the dominance even on the dominant side, as the cases that at first sight point so clearly in that direction may, perhaps, be capable of another explanation.

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* This cross was one of the first made, before the characters of the young chicks were properly appreciated.

† Unfortunately no such recessive was bred from, and it is therefore uncertain whether they would have proved pure recessives or not.

On the recessive side the evidence is even more uncertain. It became early apparent that in the case of pure *recessives*, in-breeding did not have that strong influence on the determination of dominance which it may be suggested it had in the case of pure dominants; or rather, if this effect were produced, it was much less marked. As, however, none of the actual relationships between the original White Leghorns were known, it was not at all certain that, when birds of the same strain were mated together, the offspring would be very closely bred even for one generation. Lastly, the only recessive birds yet tried, which are known to be the offspring of brothers and sisters, have not yet shown any certain increase of dominance (Experiments 51, 63, and 66).

Whether or no any of the "prepotency"* yet observed can be ascribed to in-breeding, a question which must still be left open, there is the certain fact that very distinct "prepotency" did appear on the recessive side in many instances (Experiments 43, 50, 54, 56, 62, 68, also in 74, 75, and 77, as compared with 70—73). In two of these cases also there is evidence that the proportions in successive seasons were quite different (*cf.* Experiment 54 with 55, Experiment 56 with 57), but in some others the proportions remained almost identical in successive seasons (*cf.* 70 with 71, 74 with 75). In the former case it should be noticed that in Experiments 55 and 57 the I.G. hens were old, probably in their last season of laying, and though the hens in 75 and 71 were of the same age, yet 3 years of breeding does not in the case of Leghorns nearly finish the period of fertility, and in fact such decline had not begun.

In this connection reference should be made to the interesting result obtained by Ewart† in crossing a pure Turbit with a Jacobin-Barb cross-bred female. Though not on a statistical basis, the facts arrived at distinctly support the view that with the age of the mother, the nature of her gametes changed. It is not, however, certain that this change was merely one of dominance,‡ which is the interpretation Ewart suggests. For in the light of what we now know the *cross-bred* mother must herself have been producing various gametes transmitting various characters, and the difference in the results at different ages may consequently have been due not to a change in dominance, but to the production of gametes carrying different allelomorphs (see p. 138).

A question which has been constantly kept in view is the possibility that in mixed families some proportions may be more common than others. On the hypothesis that all such mixtures point to impurity on the dominant side, it is to be expected that the average of all such cases would show the proportions equal. This expectation as regards both kinds of dominant comb compared with recessive comb is very closely realised, the totals being 459 dominant, 475 recessive. This equality may, nevertheless, have been brought about by many causes, choice of pairs, &c., and cannot be regarded as significant. The attention of those who are practically engaged in such experiments may be called to the considerable frequency of cases where equality is approached, to several cases of 3D : 2R and to several cases of 1D : 2R. The observations are yet far too few to justify any weight being laid on these occurrences, which so far seem fortuitous.

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* This word is used as signifying determination of dominance.

† 'Sci. Trans. Roy. Dub. Soc.,' 1901, vol. 7, p. 360.

‡ Supplying the Mendelian term.

Results of Breeding from Members of Mixed-first-cross Families.—On the "first hypothesis," assuming Mendel's law to be strictly followed, the results on using recessive members of mixed-first-cross families should be the same as when pure recessives were used. The only foot recessive yet tried did not give this result and therefore is plainly *not* RR as regards foot. The comb recessives, however, when bred together or with pure single-combed birds, did appear pure and incapable of transmitting the dominant character. On the second hypothesis this is the fact most difficult of explanation and is indeed entirely paradoxical.

Subsequent experiment alone can show whether the dominant comb may not again be produced; but for the present there is every indication of purity. We need not point out that the significance of such a fact in any consideration of the physiology of heredity must be very great.

Such cases, though seldom thoroughly investigated as yet, are, nevertheless, known to occur. In our own experiments one such example was seen in the stock, when there could be no question that when on crossing pure hoary and glabrous varieties, the latter (recessive) character appeared in the cross, such plants in subsequent breeding were found to be pure recessives. The famous *faux hybrides* of Millardet* are the best known illustrations of the same phenomenon.

Similarly on the first hypothesis all dominant cross-breds are to be DR, and the result of breeding from them should be the same whether they were members of mixed, or of purely dominant families, and we are to expect 3D : 1R when they are bred *inter se*. But if the second hypothesis is the true one, Mendel's law is no longer a guide, and we have no definite expectation. So far, we have only five experiments to judge from as to this point (Experiments 80—82, 85, and 87). The birds used in Experiments 80—82 were from Experiment 58, which was continued for a very short time only, giving 5 p.c. and 3 s.c. From this mixed family two pea-comb ♀ cross-breds × the same ♂ pea-comb cross-bred gave respectively 38 p.c., 22 s.c., and 46 p.c., and 21 s.c., or together 84 p.c. to 43 s.c., thus approaching 2D : 1R. But a single-comb cross-bred ♀ from the same family mated with the same male (Experiment 82) gave 34 p.c., and 50 s.c. She, however, must be supposed (p. 115) to be a pure RR, and thus we should expect equality in her offspring. Therefore we perceive that the cock was at this time almost certainly producing an excess of recessive germs ; and as the three hens used in 80—82 were all with him at the same time, it may well be this excess of recessives which has caused the numbers in 76 and 77 to depart from 3 : 1.

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* 'Mém. Soc. Sci. Bordeaux,' ser. iv, T. 4, p. 347.

On the Dorking side in Experiment 85 two dominant first cross hens from Experiment 74 were bred with own dominant brother, giving 131 rose combs to 53 single combs, or 2·47 : 1. Again the recessives are in excess, and the only other evidence as to the cock is the slight indication given by Experiment 87, where there was the expected approximate equality in a total of only 15. Taken together the four comparable totals amount to 215 D : 96 R, or 2·25 : 1. Though the departure from 3 : 1 is here decided, it cannot yet be taken as conclusive against the view that we are here dealing with DR birds, for, as has already been seen, considerable fluctuations are to be expected.

Summary of Conclusions from Experiments with Poultry.

1. When distinct breeds are crossed together certain structural characters in particular strains may exhibit the phenomenon of dominance, the antagonistic character being recessive.

Dominant characters are pea comb, rose comb, extra toe, while single comb and the normal foot are recessive. In the case of each of these pairs of characters, the cross-bred may show some blending, and as regards pea comb crossed with single, or extra toe with the normal foot, the intensity of the dominant character is often considerably reduced. In these cases, it would be possible to recognise the cross-breds *as a rule* from the dominant parents, though sometimes the dominance may be complete. The recessive form is always quite distinct.

2. When the offspring of such crosses are bred together their progeny are mixed, some presenting the dominant, others the recessive character, in proportions following Mendel's law with fair consistency, though in certain cases disturbing factors are to be suspected.

3. When some strains possessing the usually dominant character were crossed with pure recessives, this first cross resulted in a mixture of dominants and recessives. Whether in the case of comb-characters such a mixture may be taken as proving that the dominant parent was itself giving off recessive gametes, or as indicating that the usually recessive character may sometimes dominate, there is not yet sufficient

evidence to show, for some of the facts favour the first hypothesis, while others point to the second.

That the recessive foot-character may sometimes dominate was established.

4. In favour of the first hypothesis (or perhaps that of "false hybridism") is the otherwise extraordinary fact that first-cross birds with recessive combs have so far proved to be pure in that respect and incapable of transmitting the dominant comb when bred either with other similar cross-bred recessives or with pure recessives (see p. 45).

5. The relative numbers of dominants and recessives in mixed first-cross families varied greatly, but whether the degree of consanguinity in the mating by which either parent had been produced was influential in affecting these proportions was not certainly determined, though perhaps the balance of evidence is in favour of a positive influence.

6. In White Leghorns, white plumage is dominant over brown plumage, and the offspring of the first crosses bred *inter se* consisted of light and dark birds in the proportions of 3 : 1, judging by the down of the young chicks.

The dark class thus produced consists of various types, of which some are definite. A few individuals approach the dark grandparental form, while many depart widely from it, indicating that the original dark coloration is probably a compound character, capable of being broken up into component characters. The gametes, therefore, which transmit the recessive dark colours are, after crossing, of several kinds, the number of such kinds being unknown. The dark forms may be supposed to result from the union of two dark-bearing gametes, while the light birds may be supposed to result from the union either of two dominant white-bearing gametes, or of one of them with a dark-bearing gamete. Consequently the dominants (as regards plumage) resulting from the first crosses bred together are also of several types.

7. White shanks and bill are almost wholly dominant over yellow shanks and bill. The first crosses bred together give the expected mixture of whites and yellows, though in what proportions has not yet been determined.

8. There is no correlation yet perceived between the characters of comb, foot, and colour of plumage. Possibly the colour of shanks and bill has some correlation with that of plumage.

9. One definite case of distinction between the results of reciprocal matings was found (see p. 95).

[Note, added March, 1902.

So far no exception to the purity of the extracted recessive combs has occurred, but no opportunity of fully testing the purity of the recessive foot-character has yet occurred.]

PART III.—THE FACTS OF HEREDITY IN THE LIGHT OF MENDEL'S DISCOVERY.

As was stated in the introduction to this paper, with the discovery of the Mendelian principle the problem of evolution passes into a new phase. It is scarcely possible to overrate the importance of this discovery. Every conception of biology which involves a knowledge of the physiology of reproduction must feel the influence of the new facts, and, in their light, previous ideas of heredity and variation, the nature of specific differences, and all that depends on those ideas must be reconsidered, and in great measure modified.

If we turn to any former description of breeding experiments we generally perceive at once that the whole account must be re-stated in terms of Mendel's hypothesis, and that the discussions and arguments based on former hypotheses are now meaningless. As an illustration we may take the account which Darwin gives of his experiments with peloric Antirrhinum.* He crossed the peloric form with the normal and *vice versâ*. The first crosses were all indistinguishable from the normal or zygomorphic form. These were allowed to fertilise themselves, and gave a crop consisting of 88 normals, 2 intermediates, and 37 perfectly peloric. He discusses these results on the hypothesis that the normal plant has a " tendency " to become peloric, and the peloric a "tendency " to become normal, "so that we have two opposed latent tendencies in the same plants. Now with the crossed Antirrhinums the tendency to produce normal or irregular flowers, like those of the common Snapdragon, prevailed in the first generation; whilst the tendency to pelorism, appearing to gain strength by the intermission of a generation, prevailed to a large extent in the second set of seedlings. How it is possible for a character to gain strength by the intermission of a generation will be considered in the chapter on pangenesis."

Now, of course, we can perceive that the zygomorphic form is dominant and the peloric recessive, and that the arguments based on other hypotheses have no longer any significance. It would be a useful task to go similarly through the literature of breeding and translate the results into Mendelian terms. Such an exercise would show that the change which must now come over the conceptions of biology can only be compared with that which in the study of physical science followed the revelations of modern chemistry.

The outcome of such a revision of current conceptions it is impossible to foresee, but we propose in the present paper to consider some of the more important questions which are immediately raised.

To denote the new conceptions some new terms are needed. Several have already been suggested by Correns, but in practice we have not found his terminology altogether convenient, or that it meets the new requirements. Correns proposes the terms "heterodynamous" and "homodynamous" to express that an organism is dominant or not dominant in respect of a given character. There are unfortunately objections to the use of these terms, though in some respects they are very suitable. First, they are in use by Weismann and his followers in quite different senses, as Correns states. Secondly, it is not clear whether they are to be applied to the variety, the individual, or the character. Besides these objections, it is fairly clear that dominance is a phenomenon presenting various degrees of intensity; and while the single phenomenon of dominance is well expressed by that word itself, other conditions probably consist of various phenomena which are not conveniently denoted by one word.

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* 'Animals and Plants,' vol. 2, p. 46, ed. 1885.

Correns' terms "homöogonous" and "schizogonous" cannot as yet be used with precision to mean more than breeding "true" and not breeding "true," and, for reasons given later, the metaphor of splitting may be incorrect.

The terms also "*halb-identisch*" and "*conjugirte*" as applied to characters, are already fairly well expressed by the words in perfect or in imperfect correlation, which are already well understood. It would be confusing to introduce the metaphor of conjugation to denote these ideas.

But while doubting whether this terminology already suggested will be found adequate, we do not propose at present to substitute new terms for the same phenomena. In our view, there are other conceptions arising from the Mendelian discoveries for which brief expressions are absolutely required, and for these we suggest the following terminology.

In the introduction (p. 6) we attempted to distinguish precisely the essential fact discovered by Mendel, and to separate it from other subordinate appearances. We may now briefly recall and amplify that reasoning, showing how we propose to denote the several phenomena.

By crossing two forms exhibiting antagonistic characters, cross-breds were produced. The generative cells of these cross-breds were shown to be of two kinds, each being pure in respect of *one* of the parental characters. This purity of the germ-cells, and their inability to transmit both of the antagonistic characters, is the central fact proved by Mendel's work. We thus reach the conception of unit-characters existing in antagonistic pairs. Such characters we propose to call *allelomorphs*,* and the zygote formed by the union of a pair of opposite allelomorphic gametes, we shall call a *heterozygote*. Similarly, the zygote formed by the union of gametes having similar allelomorphs, may be spoken of as a *homozygote*. Upon a wide survey, we now recognise that this first principle has an extensive application in nature. We cannot as yet determine the limits of its applicability, and it is possible that many characters may really be allelomorphic, which we now suppose to be "transmissible" in any degree or intensity. On the other hand, it is equally possible that characters found to be allelomorphic in some cases may prove to be non-allelomorphic in others.

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* Correns speaks of the two opposite allelomorphs as a "*Paarling*."

It will be of great interest to determine how far the purity of the germ-cells in respect of allelomorphic characters is an absolute rule, or whether there are exceptional cases in which such purity may be impaired. That such exceptions may arise is indeed almost certain from the evidence of "mosaic" fruits in *Datura*, where it was shown (p. 23) that the otherwise pure extracted recessives (thornless) showed exceptionally a thorny patch or segment. Unless this is an original sport on the part of the individual, such a phenomenon may be taken as indicating that the germ-cells may also have been mosaic.*

Indeed all that we know of the occurrence and distribution of variation among repeated parts, would lead us to expect such a possibility with confidence.

This is a question we can analyse no further. Were it possible to do so, it might be a real help towards getting a picture of the actual process of heredity.

But besides the strictly allelomorphic or Mendelian distribution of characters among the gametes (with or without mosaics), we can imagine three other possible arrangements. (1) There may be a substantial discontinuity, the two types of gamete being connected by a certain proportion of intermediates, such as are often met with in cases even of almost complete discontinuity among zygotes. (2) There may be continuous variation among the gametes, shading from gametes pure to the one type, to gametes pure to the other type, the intermediates being the most frequent. (3) There may be no differentiation among the gametes in respect of parental characters at all, each representing the heterozygote characters unresolved. This last is the homoögonous type of Correns. By a sufficiently wide survey, illustrations of each of these systems and of intermediates between them, will doubtless be found, and the classification of gametic differentiation according to these several types, in respect of various characters, in various species, will be a first step towards the construction of a general scheme of heredity.

In gametic variation we thus meet in fact the same series of possibilities with which we have been familiar in the variation of zygotic organisms.

The second fact observed by Mendel is that each heterozygote produces on an average equal numbers of gametes bearing each allelomorph of each pair. This is only enunciated as an *average* result. Unfortunately, the determinations of the results for individuals are still few, but from those that have been made, and even from the few recorded by Mendel himself (p. 13), we see that the fluctuations are so great, that we must suspect some special sources of disturbance. Contributing to the average result of 3 : 1 as between round and wrinkled peas, he mentions as extremes 43 : 2, 14 : 15; and between yellow and green 20 : 19 and 32 : 1. It is obvious that this suggests either that there has been for some cause selection among the germ-cells originally equal in numbers, or that the numbers were originally unequal, or that the assortment of male and female germs was not governed by pure chance. Probably a series of individual determinations when seriated would throw light on the nature of these remarkable fluctuations which have been observed in almost all the subjects studied. From what we already know (see p. 121), in respect of the output of the two kinds of gametes, it is fairly certain that fluctuations take place, corresponding probably with changes in health, age, and other conditions.

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* Conceivably the cases of poultry having one foot with extra toe and one normal, may be of a similar nature, though for various reasons this is unlikely.

From analogy—an unsafe guide in these fields—and from what is known of discontinuous variation in general, we incline to the view that even though the figures point to a sharp discontinuity between dominant and recessive elements, we shall ultimately recognise that the discontinuity between these elements need not be *universally* absolute. We may expect to find individuals, and perhaps breeds or strains, and even individual gonads or groups of gonads, in which the discontinuity is less sharp even in respect of these very characters; similarly, for such units definite departures from statistical equality between D and R germs may be expected. In *Pisum*, for instance, we cannot be far out in considering an average of 50 per cent. D and 50 per cent. R as a close approximation to the truth for both male and female cells, but there is nothing yet which proves even here that the discontinuity *must be always and absolutely complete.*

Similarly, we are not compelled to accept the proposition that germ-cells of each allelomorph *always* exist on an average in equal numbers. The proofs of the two propositions are unfortunately as yet interdependent. The purity of the extracted recessives and dominants has been tested, and we can in such cases accept it as a fact: the *universal* purity of the gametes we cannot test. For, any dominant which gives rise to a recessive offspring, we should class as a cross-bred, because cross-breds are like dominants in appearance. Similarly, any partially impure recessive would be classed as a cross-bred. If the number of germs of each kind borne by the cross-bred is sensibly unequal, or the discontinuity between them sensibly lessened, we can perceive a result, but we shall not know to which cause to ascribe it. The statistical method unfortunately cannot distinguish between the two causes in such a case. Readers of Mendel's paper will be aware that he laid down no universal rule as to the absolute purity of gametes, but merely pointed out that his results were explicable on the hypothesis of such purity.

The statistics, however, are not so precise as to compel us to accept *both* that the germs of the cross-breds are *always* pure, and that they are *always* produced on an average in equal numbers.

The next point arising immediately out of Mendel's work concerns the characters of the heterozygote. In the *Pisum* cases the heterozygote normally exhibits only one of the allelomorphs clearly, which is therefore called the dominant. It is, however, clear from what we know of cross-breeding, that such exclusive exhibition of one allelomorph in its totality is by no means a universal phenomenon. Even in the pea it is not the case that the heterozygote always shows the dominant allelomorph as clearly and in the same intensity as the pure dominant, and speaking generally, heterozygotes, though in numerous instances readily referable to one or other of the allelomorphic types, exhibit those types in a more or less modified form.

Besides these, there are undoubtedly cases in which the heterozygote may show *either* of the allelomorphs, though one is commonly dominant. In the poultry crosses it was shown that the usually recessive foot-character (want of extra toe) may appear in the cross-bred. The want of dominance of hoariness in *Matthiola* seen in exceptional cases is a wholly different phenomenon (see pp. 45 and 79).

From the analogy of poultry, it is scarcely doubtful that polydactylism in man is also allelomorphic to the normal, and here from the tables of heredity already recorded,* there is good evidence that both the normal and the polydactyle offspring of one polydactyle parent can transmit the polydactylism; in other words, the heterozygote may exhibit either allelomorph. Cases of the same phenomenon can indeed be multiplied. It must, however, be remembered that what is accepted as evidence of alternative inheritance, is not a proof that the dominance of either allelomorph is imperfect. This can only be known for certain when it has already been established that individuals showing either of the two allelomorphs can, when mated with an individual showing the same allelomorph, produce both allelomorphs among their offspring.†

This leads to a point of great importance to the evolutionist We have been in the habit of speaking of a variation as discontinuous, in proportion as between it and other forms of the species intermediates are comparatively scarce when all breed freely together. In all cases of allelomorphic characters we can now give a more precise meaning to this description. It must now be recognised that such a population consists, in respect of each pair of allelomorphs, of *three* kinds of individuals*, namely, homozygotes containing one allelomorph, homozygotes containing the other allelomorph, and heterozygotes compounded of both. The first two will thus always form discontinuous groups, and the degree to which the heterozygotes form a connecting group, will depend on whether one allelomorph regularly or chiefly dominates in the heterozygote, or the allelomorphic characters completely or partially blend in the heterozygote. *Such discontinuity will in fact primarily depend not on the blending or non-blending of the characters, as hitherto generally assumed, but on the permanent discontinuity or purity of the unfertilised germ-cells.*

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* For examples see Fackenheim, 'Jen. Zt.,' xxii, p. 343.

† For the present, therefore, we are not entitled to assume that the numerous cases among Lepidoptera of varieties breeding together with a discontinuous mixed result are allelomorphic, probable as this conclusion is. Such cases are those of *Amphidasys betularia* and *doubledayaria; Aglia tau* and *lugens; Angerona prunaria* and *sordiata; Miana strigilis* and *æthiops*, &c. See Standfuss, 'Handb. d. pal. Gross-Schmetterl.,' 1896, p. 305, *et seq.*

It will be of great interest to study the statistics of such a population in nature. If the degree of dominance can be experimentally determined, or the heterozygote recognised, and we can suppose that all forms mate together with equal freedom and fertility, and that there is no natural selection in respect of the allelomorphs, it should be possible to predict the proportions of the several components of the population with some accuracy. Conversely, departures from the calculated result would then throw no little light on the influence of disturbing factors, selection, and the like.

From the circumstance that dominance of either character is no essential accompaniment of allelomorphism, it must be determined whether the proportions of the two kinds of gametes produced by the heterozygote will vary with its individual character. Bearing on this question the experiments are very few. The determination from statistical study of zygotes must be exceedingly difficult, seeing that *both* resulting forms may be heterozygous. The ratio in which the heterozygotes are distributed in the second generation need not be the same as it was in the first, and unless this can be determined it will be almost impossible to get further with this particular inquiry.

Another difficulty will be found in the possibility that when the first cross-bred generation gives a mixture, the forms showing the usually recessive character (both in this and subsequent generations) may be *pure* recessives as regards their own gametes also (false hybrids of Millardet, see p. 154) though heterozygous in origin. To solve these difficulties before the gametes can be microscopically differentiated may be still impossible.

We have now simple and convincing explanations of many facts hitherto paradoxical.

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* Four, if reciprocal heterozygotes are not identical.

1. *Heterozygous Forms.*—It has long been known to breeders that certain forms cannot be fixed by selection indefinitely continued. In other words, when the most perfect examples of such forms are bred together, though they produce some offspring like themselves, they have also a large number which do not resemble them.

A case of this kind is seen in breeding crested canaries. The kind of crest desired for exhibition can, according to canary-fanciers, be produced most easily by mating crested birds with non-crested, or plain-heads as they are called. If it be supposed that the crested character is usually dominant, we have a simple explanation. When crested birds are bred together a number of birds are produced whose crests are coarse and stand up and others without crests. The latter are the recessives; the former we may suppose to be the pure dominants. What the fancier wants is a crest composed of long feathers lying evenly down over the head. These may be the heterozygotes, and consequently cannot breed true or be fixed by selection. Such birds bred together, give many plain-heads and birds with coarse crests. Fanciers hold that the plain-heads needed for crest-breeding should be themselves crest-bred, *i.e.*, from families which have had crests among them. On the view here suggested this is probably a superstition, though one can easily see how it may have arisen.

If two crested birds are bred together it is advised that they should have imperfect crests, in all probability another form of the heterozygote.*

Another case, to which our attention was called by Mr. G. Thorne, of Broxbourne, is that of the Golden Duckwing Game Fowl. This colour can be produced by crossing Black-Reds with Silver Duckwing; but on attempting to breed the Golden Duckwing true, the colour breaks up again into its components.†

Probably the impossibility of fixing certain colours in Pigeons also illustrates the same phenomenon.

Such forms have hitherto been regarded as exhibiting "instability." Of this instability there is now a satisfactory account.

A more complex instance of this may be the Andalusian fowl. The colour is a blue-grey mixed with dull black. The breed will not continue true to colour. Though a considerable proportion of Andalusians are produced, a number will be hatched which are too dark or too light in various ways and proportions. Selecting the best Andalusians effects nothing, and the constancy does not increase. There is, therefore, a strong probability that the Andalusian is a heterozygote, though, doubtless, of a complex nature (*cf.* p. 144). Its gametes do not fully correspond to it, and its colour must be produced by a combination of dissimilar allelomorphs.

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* An account of these facts is given in Blakiston, Swaysland, and Wiener's 'Canaries and Cage Birds,' p. 128. When birds with good crests are bred together the recessive "plain-head" is often produced, a fact which has been exaggerated by various writers into the statement that the offspring of cresteds are *always* plain-heads, or even always *bald*.

† See also Lewis Wright, 'Book of Poultry,' 1886, pp. 289 and 356.

A point of great practical and theoretical importance would be the determination whether the increased vigour so commonly observed in the offspring of some crosses is or is not correlated with the union of dissimilar allelomorphs. Hitherto we have spoken of all the offspring of crossing as "crosses," alike. We must now recognise that when heterozygotes are bred together their offspring *may not be crosses at all*. The great vigour seen in the first cross is known not rarely to decline in the next generation bred from them, and it may be possible to see whether such vigour was in reality associated with the union of any recognisably dissimilar allelomorphs.

The existence of forms which are exclusively heterozygous leads to the contemplation of another possibility. In the heterozygotes we have spoken of, both sexes of course bear gametes transmitting each allelomorph. If, however, one allelomorph were alone produced by the male and the other by the female we should have a species consisting *only* of heterozygotes.

So long as the heterozygotes bred together, the offspring in such a case would come true, but a proof that they were heterozygotes would be obtained by crossing them with another species or variety. It would then be found that reciprocal crosses would not give the same result. That this is actually the case we know in certain instances, of which the most familiar amongst animals is perhaps that of the Mule (Mare × Jackass) and the Hinny (She-ass × Stallion),* and amongst plants the hybrids of *Digitalis*.† In most treatises on crossing other cases are referred to, and though probably many of them are based on experiments insufficiently repeated, there can be no doubt many are authentic. Gärtner‡ acutely observes that the phenomenon of dissimilarity between the results of reciprocal crosses is more likely to be found among diœcious forms.

2. *Selection and the Phenomenon of Dominance.*—We have seen that the want of fixity in certain forms, though continually selected, may at once be explained by the hypothesis that they are heterozygous only, and have no gametes corresponding to them. Another illustration of the failure of selection is the constant recurrence of a particular "rogue" in the best strains. Seed is never taken from such rogues. Every year they may be pulled up as soon as detected, but they continually reappear.

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* A good description of the differences between these forms is given by Cornevin, 'Traité de Zootechnie,' 1891, p. 641.

† See Focke, 'Pflanzenmischlinge,' 1881, p. 322; and Gärtner, 'Bastarderzeugung,' 1849, p. 225. Other examples are given by Gärtner, *ibid.*; and by Swingle and Webber, 'Year-book Dept. Agric.,' 1897, p. 401.

‡ *Loc. cit.*, p. 228.

The hypothesis that such a "rogue" is a recessive form *may* give a complete explanation of this phenomenon in many cases. Selection from *individuals* of known fertilisation would at once test the truth of this view, and might provide a means of producing a pure strain once and for all from the pure dominants.

It is well known that some of the best modern beardless wheats which have been raised of late years by crossing distinct varieties will give a small proportion of bearded plants. This is, of course, called "reversion" to a bearded ancestor used in the original cross.

From the experiments of Rimpau,* we find that when bearded and beardless varieties are crossed, beardlessness is dominant, and the bearded character is recessive. By subsequent breeding a form is produced with a desirable character, and after a few years of selection it is found to give this character with sufficient purity and it is put on the market. It may be a bearded or a beardless form, but if the latter, the chances are that it will always produce a certain proportion of bearded plants.† This may happen in every case where there has been a *promiscuous* selection of many dominant plants, for any one of these may be a heterozygote and bear in each year both dominant and recessive germs.

The fact that the hornless breeds of goats still give some horned offspring is probably referable to the same cause. The point is of course not certain, but from the analogy of cattle (see p. 140) we may anticipate that the hornless form is dominant. In the polled breeds of cattle, which are never *promiscuously* selected, the polled character has naturally been easily fixed pure, but in goats selection among the *ewes* has been probably to a large extent promiscuous.

The phenomenon is without doubt occurring very widely in nature. To it we may perhaps attribute the undiminished persistence of some weakly varieties, which are unceasingly exterminated by natural or artificial selection without ever leaving offspring. Cases have only to be looked for to be found in abundance. We may note the paradox that, for anything we know to the contrary, a recessive allelomorph may even persist as a gamete *without the corresponding homozygote having ever reached maturity in the history of the species.*‡ It would be premature to trace out the deductions to which this suggestive fact points, but we see at once that it may give the true account of the phenomenon that domesticated forms constantly give rise to varieties not met with in the wild state, a fact often ascribed on insufficient grounds to the action of changed conditions in producing greater *variability*.

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* 'Landw. J. B.,' 20.

† Such a variety is Garton's Red King.

‡ [In illustration of such a phenomenon we may perhaps venture to refer to the extraordinarily interesting evidence lately collected by Garrod regarding the rare condition known as "Alkaptonuria." In such persons the substance, alkapton, forms a regular constituent of the urine, giving it a deep brown colour which becomes black on exposure. The condition is exceedingly rare, and, though met with in several members of the same families, has only once been known to be directly transmitted from parent to offspring. Recently, however, Garrod has

It will be clear—a point which may have some economic importance—that in any such case the recessive "rogue" can be eliminated by selection from *individual* plants or animals, breeding only from those which give no recessives on being self-fertilised, if hermaphrodite. If the organism be diœcious the process will be more elaborate, for it will be first necessary to test for recessive allelomorphs by fertilising with a recessive, and afterwards to fertilise those that gave no recessive offspring, with a dominant similarly proved to be free from recessive influence. Nevertheless it is certain that by this process alone can a strain of pure dominants be readily made.

"Purity" then acquires a new and more precise meaning. An organism resulting from an original cross is not necessarily pure when it has been raised by selection from parents similar in appearance for an indefinite number of generations. *It is only pure when it is compounded of gametes bearing identical allelomorphs, and such purity may occur in any individual raised from cross-bred organisms.*

An organism can be strictly defined as genetically pure if all its gametes when united with similar gametes reproduce the parent identically; and in practice the only way in which such purity can, by one breeding, be tested, is by crossing the organism in question with pure recessives.

There are also other classes of cases where progressive selection fails not only to fix a particular variety but to diminish the proportion of "rogues" beyond a fairly definite limit. We may first consider how far the principle of dominance may give an acceptable account of such cases.

In his most valuable book, 'Die Mutationstheorie,' 1901, Professor de Vries devotes a chapter to the consideration of such phenomena, pointing out in a number of cases that progressive and continued selection has failed to fix a particular character. He draws the conclusion that such characters distinguish "half-races," as he calls them, which cannot be bred pure.

noticed that no fewer than five families containing alkaptonuric members, more than a quarter of the recorded cases, are the offspring of unions of *first cousins*. In only *two* other families is the parentage known, one of these being the case in which the father was alkaptonuric. In the other case the parents were *not* related. Now there may be other accounts possible, but we note that the mating of first cousins gives exactly the conditions most likely to enable a rare and usually recessive character to show itself. If the bearer of such a gamete mate with individuals not bearing it, the character would hardly ever be seen; but first cousins will frequently be bearers of *similar* gametes, which may in such unions meet each other, and thus lead to the manifestation of the peculiar recessive characters in the zygote. See A. E. Garrod, 'Trans. Med. Chir. Soc.,' 1899, p. 367, and 'Lancet,' November 30, 1901.]

The cases taken are many-leaved clovers, a polypetalous Ranunculus, several plants with variegated foliage, and the biennial forms of certain species.

Selection in each case at first rapidly increases the proportions in which the selected form appears among the offspring, but soon a maximum effect is produced which is not surpassed.

Now in each of these examples fertilisation was left to insects, and though seed was saved from individual plants it is not in dispute that cross-fertilisation between them occurred. In Mendelian terms some might be pure D, some pure R, and some DR. Supposing dominance complete, eradication of the pure R forms annually does not extinguish them, for by the breeding of the DR forms *inter se* they will be continually reproduced.

There are no doubt many overlying complications in each of these cases, as, for instance, the probability that dominance is in these instances imperfect, but these will not change the main result.

The case of the biennial plants is especially interesting, as here we have strong indications that treatment and conditions may determine which character shall appear. For example, de Vries quotes the evidence of the Sugar Beet, a plant of great economic importance, to the breeding of which much attention has been devoted.

The plant which forms the large sugar-bearing axis is a biennial and does not flower until it has made the sugar-store. But from the best seed which has for generations been saved from such plants only, there arises a small percentage of an annual form which runs to seed without making a thick root at all. After years of selection the proportion of such rogues is not diminished. Now, if it could be supposed that the annual is recessive and the biennial dominant, this is partly explained. On selection, seeds are taken from dominants only. But some of these will be pure dominants and others will be heterozygotes bearing *both* allelomorphs. The latter will each year give rise to a certain number of pure recessives, compounded of two recessive gametes. In the first years of selection, the proportion of recessives will be diminished rapidly by choosing seed from dominants only, but further *promiscuous* selection of dominants, unless continued for an indefinite time, will not altogether remove the recessives, for they arise from the dominants themselves.*

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* It is of course only a conjecture that the biennial form is dominant in these cases, but, owing to the great importance of the subject, it seems worth while to call the attention of those interested to the possibility. Among the many investigations already made on the Beet it does not appear that the simple experiment has been tried of seeing if the annual or biennial form can be bred true from *individual* plants fertilised under proper precautions. Still less has the possibility of dominance been investigated. The only evidence known to us is that of Rimpau, that when the annual *Beta vulgaris* was grown near the cultivated form it bore two seeds which proved biennial and fifty-eight which were annuals. Rimpau

But in these forms it is well known that several kinds of treatment, exposure of the young plants to frost, over crowding, heavy manuring, and forcing, will greatly increase the proportion of "runners." In the case of *Œnothera* de Vries has made some very convincing experiments, clearly proving this fact, and Rimpau has done the same for the Beet, showing that the number of "runners" can thus be greatly increased. There are then some which are biennial in any case, some which are biennial or annual according to treatment, and some which are in any case annual. This is strongly suggestive of the three Mendelian classes.

De Vries has also experimented by selection from the annual plants, getting of course a higher proportion of annuals. But it must be remembered that in order to prove that the annual character is recessive, and that it can, as such, be fixed by one selection, it is necessary to ascertain first that the plant chosen is not what de Vries calls a "facultative" annual—on this hypothesis, a DR—and secondly that it has not been cross-fertilised, particulars not yet forthcoming.

But even if the hypothesis of dominance could be successfully applied to these cases, there are others at first sight similar, where it cannot be thus applied; for example, instances of varieties recessive in their differentiating character, producing annually a small but sensible number of a particular "sport," exhibiting a character already known to be dominant. Here we must suppose either that we meet the phenomenon of an *originating* variation—the "mutation" of de Vries: or possibly, which appears to be de Vries' view of half-races—the output of a certain number of such aberrant gametes is normally incidental to the development of the type-gametes. An objection to the latter deduction in some cases exists in the fact that the "sports" in question may be exceedingly rare, and therefore produced by few individuals only.*

3. *Skipping a generation.*—That marked individual peculiarities fail to appear in the immediate offspring, but may reappear in a subsequent generation has been often observed, and the fact has taken a great hold on the popular imagination. It has not yet been shown that the distribution of any of these characters among the different generations in any line of descent is other than is to be expected on the hypothesis of pure chance. Nevertheless we have now in the phenomenon of dominance a fact which may possibly be a real element

conjectures that the two were crosses with the cultivated form, in which, as we should now say, the latter was dominant. But *B. patula*, an annual, emasculated and fertilised by cultivated Beets promiscuously, gave annuals only. Here there is a cross with another species, and the evidence is of doubtful application.

* Excellent illustrations of this phenomenon in the case of high-class Peas have been lately supplied to us by Mr. Arthur Sutton. Of these we hope to give details hereafter.

in the causation of such appearances, and those who are familiar with statistics of inheritance, in man for example, might usefully study them with the possibility in view. The absence of the character in the first generation may indicate merely that it is recessive, and its reappearance in the next generation may be due to the heterozygote having bred with another individual also bearing the recessive allelomorph.

4. *"New" characters may be dominant.*—We cannot as yet perceive any properties common to dominant as compared with recessive characters. It will be noted, however, that the view of many naturalists that the phylogenetically older character is prepotent, or, more correctly, dominant, is by no means of universal application. In poultry, for instance, both pea and rose combs are dominant against single, though the latter is almost certainly ancestral; the polydactyle foot is dominant against the normal, though a palpable sport. A point of some interest is that in both wheat and barley the beardless form is dominant, though we naturally, though perhaps incorrectly, regard it as a state normal in the one species, but an innovation in the other.

In cattle the polled form is dominant over the horned, though the former is a character which in our cattle has certainly arisen since domestication.

5. *Prepotency.*—The conception of dominance avoids certain difficulties which are involved in the use of the term "prepotent." As we now know that the allelomorphs of the several characters may be quite independent, it is confusing to speak of the prepotency of an individual when all that we know is that one or more of its characters is dominant over the contrary character. Of the dominance or prepotency of the *whole* we know nothing. The diversity of the views which have been at various times expressed as to the respective powers of mother or father to confer special qualities has probably arisen from confusions thus caused. If the term prepotency is to be preserved it must be applied to characters rather than to organisms, and its use must be restricted to cases in which the character so qualified has been actually tested by combination with the contrary allelomorph in one heterozygote.

We have been accustomed to consider that a variety may be sometimes prepotent in respect of a given character and sometimes not prepotent. The whole evidence on which this view is based will in many cases now require careful verification, for, as was fully discussed in the case of poultry, such a result may really be due to an unsuspected heterozygote having been sometimes used for the other parent. The evidence, for instance, that on crossing pea comb and single comb the offspring may be sometimes pea and sometimes single would formerly have been thought a clear proof that pea comb was not always dominant, whereas it is now certain that much fuller evidence is needed to establish this proposition.

The existence of the so-called "false" hybrids of Millardet (see p. 154) is an even more serious difficulty besetting the conception of prepotency, for here, though the cross-breds are produced by a union of the male and female gametes of two varieties, it is quite uncertain that the characters of both parents are introduced at all. (See p. 155.)

As a rule fair uniformity prevails among the results of first crossings, and in every case in which a mixture of forms occurs the question must now be asked *whether the fact is not a proof that either or both of the parents are actually producing more than one sort of gametes.* It is, no doubt, possible to conceive of the elements contributed by the two gametes respectively as engaged in a conflict so balanced that some supervening circumstances may give dominance to either side with varying frequency; but from what we now know of the nature of heredity, the conception of dissimilar gametes borne by one or both parents is just as easy to form, and no less probable on the facts.

6. *Sex.*—It is often profitable to compare the phenomena of variation with those of sex, and if the suggestion alluded to in the last paragraph be found true, it is worth reflecting whether the determination of sex may not sometimes be a phenomenon similarly conditioned.

[Note, added March, 1902.

There is already a considerable body of evidence in favour of the view that difference of sex is primarily a phenomenon of gametic differentiation. The evidence, however, seems to point to the conclusion that the differentiation is sometimes a phenomenon of the male cells and sometimes of the female cells, sometimes perhaps of both. Our attention has been called to a note by McClung,* suggesting that the differentiation of the spermatozoa of many insects and of some other Anthropods, according as they do or do not contain the "accessory chromosome," may be an indication of differentiation in regard to sex. This body has been the subject of extensive study on the part especially of the American cytological investigators, and further researches regarding it may be a most profitable field of inquiry.

The fact that in *Nematus ribesii*,† and in the Hive-bee, the unfertilised eggs produce males only, seems to prove that in those cases the female cells are carriers of the male character only, though whether there is sex-differentiation of the male cells is not yet known.

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* 'Anat. Anz.,' November, 1901, p. 220.

† Professor Miall has given me a reference to Cameron, 'Phytoph. Hymenop., Ray Soc. Monogr.,' vol. 1, p. 26, where authorities are quoted. He tells me that the same result was obtained in experiments of his own.

On the other hand, we have more frequent cases of unfertilised eggs in other types producing females only.

But from the observations of de Buzareingues,* it appeared that there is a more or less definite distribution of the sexes among the seeds of diœcious plants, the females being more commonly derived from seeds of one region, and the males from those of another. This of course is no proof of *original* differentiation of sex among the female cells, but it is readily consistent with that hypothesis.

On the other hand, as on the whole *against* the hypothesis that sex depends chiefly on gametic differentiation, may be mentioned observations—especially those of Wichura ('Bastardbefruchtung,' p. 44)—that the statistical distribution of sex among first crosses shows great departure from the normal proportions. The same has been seen by many hybridisers using animal types. But the further fact that there is a still greater variation in the statistical relations of the sexes in the *offspring* of hybrids, is rather favourable to the hypothesis.

The frequent occurrence of hermaphrodites among *first* crosses is also difficult to explain on the present hypothesis.]

7. *Reversions.*—With the Mendelian conception of the heterozygote as a form with its own special "*hybrid character*," we have a *rationale* of large numbers of "reversions"; for we already know many cases where heterozygotes do present the characters of putative ancestors. This fact reduces to harmony several groups of results where different experimenters, believing themselves to have worked with similar organisms, have reached seemingly contradictory conclusions. For some have used pure forms and others heterozygotes appearing in their guise.

THE NATURE OF ALLELOMORPHISM.

A. *Simple Allelomorphs.*

The following list enumerates the principal cases in which the phenomenon of allelomorphism has either been actually proved to exist or may be safely inferred from the published records.† In each of these cases more or less definite dominance of one character has been found, and in this list the dominant character is put first :—

1. Hairiness and absence of hairs (Lychnis).
2. Hoariness and absence of hairs (Matthiola).
3. Felted ears and smooth ears (Wheat).‡

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* 'Ann. Sci. Nat.,' vols. 16, 24, and 30; 1829, &c.

† [From the evidence of crosses kindly carried out for us by Mr. Leonard Sutton we are able to add the "palm" leaf (palmatifid) and reddish stems of *Primula sinensis* as dominant characters, while the "fern" leaf (pinnatifid) and purely green stems are recessive characters.—March, 1902.]

‡ Rimpau, 'Landw. J. B.,' 20, 1891, p. 346.

4. Prickliness and smoothness of fruits (Datura).
5. Style long and short (Œnothera).[*]
6. Beardless and bearded ears (Wheat and Barley).[†]
7. Pointed seed and rounded seed (Maize).[‡]
8. Round and wrinkled seed (Pisum).
9. Starch endosperm and sugar endosperm (Maize).
10. Inflated (generally hard) pods and constricted (generally soft) pods (Pisum, Phaseolus).
11. Axial distribution of flowers and terminal distribution of flowers (Pisum).
12. Tall habit and dwarf habit (Pisum, Phaseolus), to which, from experiments seen at Messrs. Sutton's, we think we may safely add tall habit and dwarf procumbent habit (known to gardeners as "Cupids") in Sweet Peas (*Lathyrus odoratus*).[§]
13. Entire petals and laciniated petals (*Chelidonium majus*).[||]
14. Normal zygomorphic form and peloric form (Antirrhinum[¶] and probably Linaria).[**]
15. Normal habit and waltzing habit (connected with malformation of the aural labyrinth) (Mouse).[††]
16. Presence and absence of extra toe (Fowl).[‡‡]
17. Pea comb and single comb (Fowl).
18. Rose comb and single comb (Fowl).
19. Polled and horned breeds (Cattle and probably Goats).[§§]

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[*] De Vries.

[†] Rimpau, *loc. cit.*, pp. 341 and 353. Since this paper was written we have received Tschermak's valuable analysis of the phenomena in regard to wheat, which considerably extends our knowledge of allelomorphism in that species (see 'Ztsch. für d. Landw. Versuchswesen in Oester.,' vol. 4, 1901, p. 1029.

[‡] Correns, 'Biblioth. Bot.,' vol. 53, 1901

[§] Some distinct exceptions to the rule of dominance of the tall form are already known. [See final note.]

[||] De Vries.

[¶] Darwin, 'An. and Plts.,' ed. 2, vol. 2, p. 45.

[**] In the case of *Linaria*, Naudin found that on crossing a peloric *Linaria* with a normal one a mixture of normal and peloric plants resulted. As to the origin of the peloric parent there is no information, and consequently it may have been a heterozygote. See Naudin, 'Nouv. Arch. du Mus.,' 1865, I, p. 137.

[††] Von Guaita, 'Ber. Natur. f. Ges.,' vol. 10, 1898, p. 317, and vol. 11, 1899, p. 131. For reference to this interesting case we are indebted to Professor Correns.

[‡‡] The allelomorphism is not yet fully proved in this case. It is the only obviously meristic character in which there is yet any evidence of allelomorphism.

[§§] It is almost certain that absence and presence of horns are allelomorphic characters. In England there are three principal polled breeds of cattle—the Aberdeen-Angus, Galloway, and the Red Polled. The first two are black, the last red. Between these and the horned breeds crosses are annually made in large numbers. This is especially the case with the Angus, from which great numbers of cross-bred cattle are annually bred for the meat market. These are usually Angus-Shorthorn crosses, but other horned breeds are also occasionally used. The

20. White shanks and yellow shanks (Fowl).
21. White plumage and general brown coloration (Fowl).*
22. Several coloured forms of flowers and their white varieties.
23. Several colours of fruits and their xanthic varieties (Atropa, Solanum).
24. Several colours of seed coats.
25. Darker and lighter colours of endosperm (Maize).
26. Yellow and green cotyledons (Pisum).

With regard to seed-colours, Correns has shown that the question is a complex one, depending on several factors. In Maize, especially, the seed-skin and the several parts of the endosperm may all be independently concerned in giving the net result. Each must be considered separately, and in several cases the dominance is imperfect, and blendings may occur.†

Between various simple allelomorphs correlations may of course occur. A few of these we know already. But in these cases of simple

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cross between a pure Angus and a pure Shorthorn is almost always a blue-grey without horns. Generally the horns are represented by loose corns of horny material, sometimes imbedded in the skin and not rarely hidden by the hair. Such "scurs," as they are called in the north, are objected to in the pure polled breeds and are mostly absent.

Notes of the cross-breds exhibited at the Smithfield Club Cattle Shows in 1888, '89, '98–'01 give the following results. The animals are classified according to the descriptions in the Catalogue. No doubt, however, the actual purity of the parent breed or breeds was in many cases doubtful. Taken as they stand, the numbers exhibited in these six years were as follows :—

$$\text{From}\left\{\begin{array}{l}\text{Polled Angus}\\ \text{Polled Galloway}\\ \text{Red Polled}\end{array}\right\}\times \text{ some horned breed, usually Shorthorn, and the}$$

reciprocal cross—104 polled, 13 horned.

From first cross animals bred as above, mated with a pure polled parent—23 polled, 1 horned.

From first cross animals mated with some horned parent—18 horned, 24 polled.

When allowance is made for the very rough materials out of which these figures come, it is clear that the facts cannot be very far from the Mendelian expectation. It is, however, likely that the allelomorphs concerned are not merely the horned character in its entirety, and total absence of horns. For in the offspring of (polled × horned) × polled, the horns, when they occur, are often *loose* though of fair size. If all parts were completely correlated we should expect *either* absence of horns (perhaps mere scurs) *or* ordinary horns like those of horned breeds. Probably, therefore, there is not *complete* correlation between the formation of horns and that of the bony cores which carry them, and these characters are divisible in transmission. Unfortunately the cross-breds are practically never bred together, so the valuable evidence thus attainable is wanting. It should be mentioned that in offspring of (polled × horned) × horned the coat-colour character also breaks up.

* [Wh. Dorking × Ind. Game crosses are this year giving exceptions to dominance of white.—1902.]

† Full details given in Correns' memoir, 'Biblioth. Bot.,' 1901.

correlation the gametes may each transmit the correlated groups or the opposite allelomorph entire (see case of Matthiola, p. 81).

From the foregoing list it appears that allelomorphism may occur in a great diversity of characters, involving many different physiological factors.

In the plants albinism appears to be recessive, but in the case of fowls white plumage is dominant, though not completely so. It does not appear as yet that simple allelomorphism occurs between any two colours, of which neither is xanthic or albino.

B. *Compound Allelomorphs.*

So far, in all or nearly all the cases we have considered, the dominant and recessive characters are each *simple.* In other words, when the heterozygotes breed together, they produce dominants and recessives like their parents, heterozygotes like themselves, and no other forms. The gametes therefore respectively bear characters which are the same as those of the varieties which were used to produce the heterozygotes. We have next to consider a numerous and important group of cases in which a character of one of the original parental varieties after crossing is itself split up. Of these we will give illustrations.

1. *Sweet Pea.*—By the great courtesy of Messrs. Sutton and Sons we have been permitted to watch many of the experiments conducted at their nurseries. We cannot sufficiently express our indebtedness for the splendid opportunities of study in these fields thus provided. For the most part these phenomena are not dealt with in the present paper, and amongst many interesting results there witnessed we propose now to refer very briefly to the following only:—

Sweet Pea (Lathyrus odoratus).—Stanley, standard dark maroon or chocolate, with wings similar but somewhat tinged with violet, crossed with Giant White, gave *all* Giant Purple Invincible, viz., standards as in Stanley, but wings blue. These first crosses self-fertilised, gave Giant White, Giant Purple (without blue wings), Mars (a well-known red variety), Her Majesty (a full magenta, well known), and a form like Her Majesty, *but flaked with white.**

One plant of each was saved and its self-fertilised seed sown. Mars and Her Majesty came true. The Giant White was tested, and it came true also. The Her Majesty flaked with white, however, gave Whites, Her Majesty, and Her Majesty flaked white again. The Giant Purple gave Giant White, Her Majesty, Giant Purples, and two plants of a streaky cream colour.

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* It is possible that this complex result does not always occur; for in another case a Giant Rich Purple, very like Stanley, crossed with Giant White, gave seedlings *all* Giant Rich Purple. These on self-fertilisation gave a mixture of Giant White and Giant Rich Purple again. One plant of each on self-fertilisation gave only offspring like itself.

The facts point to a higher degree of complexity than we can yet realise, but we see that the first crosses are all alike, though differing from the coloured parent. The same form, or something very like it, was often observed to come in other cases where a blue or purple parent was used in crossing. Now on self-fertilisation the first cross gave a variety of forms. It therefore produced a variety of gametes, not two kinds, but several. Of these forms some, Mars, Her Majesty (Giant White also in all probability), reproduced themselves exactly. Therefore they had only one kind of gamete, and they must be supposed to have been formed by the union of similar gametes. The purples, on the contrary, produced most of the whole series again, showing that they were producing a variety of gametes like the first cross parent itself.

Her Majesty flaked with white, gave some Her Majesty, some White, some Her Majesty flaked white. Therefore the flaked plants are heterozygotes, formed by the union of a Her Majesty gamete with a white gamete.

We are then led to the conclusion that the allelomorph transmitting the coloration of Stanley is *compound*, and that it can be broken up into simpler and possibly component elements. When *similar* elements, thus extracted, combine in fertilisation, they do not split up again on the formation of gametes. The constituents of the compound allelomorphs may perhaps be spoken of as *hypallelomorphs.*

The fact that Stanley did not occur again is another indication that its colour character had been broken up into *more than two* elements.

Another fact which may point in the same direction is that the purple formed on the first cross is different from that which recurs in the next generation. In fact, this Giant Purple Invincible results from the union of the whole compound allelomorph of Stanley with that of Giant White. We may suppose that it does not come again for the reason that the compound allelomorph has been broken up among the gametes borne by the first cross, and that the union of no two of these, or of any of them with white, results in that particular heterozygote form, Giant Purple Invincible. Inasmuch, however, as Giant Purple Invincible, not yet distinguishable from that produced in this cross, is a well-known and stable form, there must *either* be gametes corresponding to it* (or its male and female gametes must be dissimilar and combine in that definite heterozygote, which is most unlikely). Till the experiment has been repeated on a large scale we must not lay much stress on the absence of Purple Invincible after the break up of the first cross, because in other experiments where White Cupid (a procumbent form) was crossed with Mme. Carnot (a blue), Purple Invincible again resulted together with White Cupid (? the result of imperfect emasculation). These Purple Invincibles, self-fertilised, gave several forms, amongst them Mme. Carnot and some Purple Invincibles again. Whether this indicates that the compound allelomorph is not wholly broken up, or that its character may again be synthetically reproduced, cannot yet be said. Corroborative evidence that the blue elements are definitely extracted from the "derived" Her Majesty was seen in the fact that this variety when crossed with various pink and cream kinds gives no blues or purples.

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* Similarly from other crosses seen at Messrs. Sutton's it is clear that the form called "Painted Lady" may be another heterozygote form, though the same is one of the oldest and most familiar fixed forms. According to Mr. S. B. Dicks, there is good reason to believe the purple and the Painted Lady forms to be the oldest varieties. 'Report of Sweet Pea Conference,' 1900.

To the whole subject of the results of crossing Sweet Peas we hope to return when our own experiments are further advanced.

The probability is that in this, as in other similar cases of compound allelomorphs, there is a heterozygote form which may be common to several combinations of dissimilar gametes, and it is characteristic of such forms that they may reproduce *in appearance* some putative ancestor. It is to this class of phenomena that Darwin's famous "reversions on crossing" are probably to be referred.

2. *Poultry.*—Another example of the splitting up of a compound allelomorph is probably to be seen in the poultry experiments. The first cross between Indian Game and White Leghorns, for instance, is white flecked with a few black or grey feathers, sometimes barred, sometimes irregularly marked with pigment. Such first crosses bred together give some dark birds and some light (see p. 108), the latter being sometimes pure white, sometimes flecked with black, and sometimes pile (brown and white). When White Dorkings are crossed with Brown Leghorns the result is very similar; but in each of these cases the dark birds resulting from the inter-breeding of the first crosses are not simply like their dark grand-parent, but belong to several distinct types of coloration such as black, cuckoo, silver-grey,* together with some more or less nearly reproducing the dark grand-parental type. The numbers reared are far too small to justify a comprehensive deduction, but that the types of coloration thus produced have some definiteness is quite clear. Whether any of them will breed pure must be unknown till next season. As already stated, some of these colours are already well known as characterising various breeds.

Until experiments have been carried out with the express object of proving the compound nature of allelomorphic characters and of resolving them into their constituents, we can only gather indications of such phenomena from experiments undertaken for other objects. Of these there are a considerable number which leave little doubt that further examination would disclose such a result. We may mention the observations of von Guaita on mice, from which it appeared that the first cross of albino mice with black-and-white Japanese waltzing mice, gave a grey house-mouse resembling in size, colour, and wildness the wild house-mouse.* The first crosses bred together gave albinos, grey mice, black and white, grey and white, and black mice (with the waltzing character distributed among them in proportions closely obeying the Mendelian ratio); of these the albinos produced, with one exception, albinos only when bred together. The grey marked with white, bred together, produced no more blacks or black-and-whites; and the blacks and the black and whites bred together gave no more greys, though both descriptions may still give albinos. Facts like these strongly suggest that, with suitable mating, the classes could be shown to consist of the original albino, and a number of forms, some of which would henceforth be pure, while others would be found to be heterozygous.

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* The appearance of silver-grey in the offspring of first crosses between White Dorking and Brown Leghorn may be attributed to the certainty that White Dorking were related to Silver-grey Dorkings. The colour may, nevertheless, have come from resolution of the Leghorn colour, for it is not peculiar to Dorkings, but is known in other breeds, *e.g.*, Game Duckwings.

3. Another case, possibly of the same nature, is that of the Himalayan rabbit, of which an account is given by Darwin.†

The literature of pigeon-fancying abounds with information pointing to a similar *rationale* of the colour phenomena there seen. Formerly the recipes given in such treatises as to the methods of mating to be followed for the production of particular colours would have seemed mere nostrums, but now we can see at least the general basis of fact whence they have been derived.

The experiments with stocks described (p. 81) give cases probably also analogous. Several forms crossed together all gave purple for the first cross, which on being self-fertilised gave other colours in addition to those of the pure parental forms and that of the first cross.

This conception of compound allelomorphs is almost the same as that which Mendel himself introduces in speaking of his Phaseolus crosses.‡ His analysis does not, however, seem to be strictly correct, and the subsequent reasoning is consequently obscure and not altogether valid. He says if the colour of the red Phaseolus be made up of $A_1 + A_2 + \ldots$, then on crossing with a white form a, hybrid unions are produced, $A_1a + A_2a +$ &c.

But it is the group $A_1A_2 \ldots$ which is allelomorphic to a, and the heterozygote is $A_1A_2 \ldots a$, and not $A_1a + A_2a +$ &c. It cannot be till the crosses form their gametes that the compound allelomorph breaks up.

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* Haacke, crossing albinos with grey-and-white Japanese waltzing mice, usually obtained the same result, viz., grey mice, but more rarely *black* mice. The latter result must be taken as indicating impurity in one or other parent. Vosseler, quoted by von Guaita, obtained greys only. See Haacke, 'Biol. Cblt.,' vol. 15, 1895, p. 45.

† 'An. and Plts.,' I, p. 113.

‡ *Loc. cit.*, p. 35.

It is not evident how this error of expression came about. Mendel in consequence misses the point that by the breaking-up of the compound character after the cross, new fixed forms may be produced by union of the elements of the original compound allelomorph, without any admixture from the variety with which the first cross was made. Such pure forms may be represented as A_1A_1, A_2A_2, &c., and of these we have already seen instances in the case of the Sweet Peas, Mars and Her Majesty.

Of the coloured forms appearing as offspring of the first crosses inter-bred, some are compounded of colour-bearing gametes meeting similar or dissimilar colour-bearing gametes, and some (like the Sweet Pea, Her Majesty, flaked with white) of a colour-bearing gamete meeting a white-bearing gamete.

We have good reason to believe that the compound allelomorph is not in every case resolved into its ultimate constituents when the gametes of the first cross are formed, and indeed we must suppose such imperfect resolution to be present whenever, as in the case of the Sweet Pea, among the resolved forms (White, Mars, Her Majesty) there occur complex heterozygotes like Giant Purple, which can itself produce a series of forms in the next generation. Such a form may be represented as $A_2A_3 \ldots a$. It is to this class of complex heterozygotes that we conceive the Andalusian fowl to belong.

It is doubtful whether and in what sense we are entitled to regard the whole compound character as *one* allelomorph. Some justification for this conception is to be found in the fact that in the poultry crosses the light chicks bore to the *whole number* of dark chicks the proportions of 3 : 1. On the Mendelian hypothesis this must be taken to show that the cross-breds produce on an average white-bearing gametes equal in number to the whole number of colour-bearing gametes, which may bear the colour-allelomorph in various stages of resolution.

By statistical investigation of such cases it should be possible to determine with some success how the unresolved characters are related to the elementary characters, and to make a scheme of *equivalence*.

It is, perhaps, hardly too much to suggest that in a great number of cases the familiar fact so often observed that first crosses bred together give a profusion of new forms may be capable of similar explanation. With such new forms the usual experience is that some breed true from the beginning, while some continue to give rise to other forms, of which some may have already been produced, while others again are new. The cases we have taken are those of colour-varieties, as the facts in those cases are clearer, but their nature is probably not different. It is in this sense that crossing may be truly spoken of as a "cause" of variability, and some picture of that phenomenon is now provided.

The importance of this reasoning lies in the fact that we can now recognise that these different new forms may be, in their genetic composition, diverse. We are no longer to expect that it is a matter of chance whether each will be able to transmit any of the other forms, but we perceive that this is a question to be determined by actual observation once for all. When such determinations shall have been made on a statistical basis we shall be able to state precisely the numerical proportions which the gametes of the several classes bear to each other, and hence to determine the actual number of constituents of the compound allelomorph and their relationships to each other. This investigation is now merely a matter for precise quantitative analysis.

Remembering that we have no warrant for regarding any hereditary character as depending on a material substance for its transmission, we may, with this proviso, compare a compound character with a double salt, such as an alum, from which one or other of the metals of the base can be dissociated by suitable means, while the compound acid-radicle may be separated in its entirety, or again be decomposed into its several constituents. Though a crude metaphor, such an illustration may serve to explain the great simplification of the physiology of heredity to which the facts now point.

A marked feature in connection with compound allelomorphism* is the frequency with which in such cases one or more of the heterozygotes present what we have reason to regard as ancestral characters. To such "reversion" we referred in speaking of Sweet Pea crosses. The Sweet Peas produced a flower with purple standard and blue wings approaching what we may regard as a primitive Sweet Pea. Several white varieties of Stock produce a purple form; many of the crosses with the "half-hoary" type gave fully hoary heterozygotes. The Albino and Japanese mice produce a grey house-mouse as their heterozygote. *Why* such heterozygotes should show ancestral characters we do not know; but we can now recognise that such "reversions" are heterozygous mixtures and not constant forms. To speak of such reappearances of ancestral characters as a reappearance of the ancestral *form* is entirely misleading. These heterozygotes will not breed true, and *are* ancestral in no real sense. Not only are they heterozygous and in constitution compound, but, as in the Sweet Pea, several different compounds agree in having the same ancestral form as their specific heterozygote.

It is unfortunate that Darwin's own experiments with poultry and pigeons were so complex that it is now impossible to disentangle the results or to use them for the purposes of these deductions. He records the most complicated unions of birds of different breeds, some homo-, some hetero-zygotes, some exhibiting simple and others compound allelomorphs, and in the statement of results the all-important distinctions between the generations and the offspring of the several individual birds are often not observed.

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* There is no reason for supposing such reversion to be absent in all cases of heterozygotes formed by the union of *simple* allelomorphs, but the few clear cases known seem to be all cases including compound allelomorphs.

To sum up the phenomena of compound allelomorphism, we may say that the evidence shows that the characters of a pure form when crossed with another may be broken up into component characters or hypallelomorphs, and that the decomposition may take place in various degrees of completeness.

To the variations which thus arise by resolution of compound characters we propose to give the name *Analytical Variations.* There can be no doubt that a very large proportion of the discontinuous variations in colour, at all events, met with both in wild and domesticated species are of this nature. The fact that similar component forms are similarly related to each other and to the type, in various species, thus provides the true account of numerous phenomena of "parallel" variation.

The facts thus grouped, suggest the following questions. Has a given organism a fixed number of unit-characters? Can we rightly conceive of the whole organism as composed of such unit-characters, or is there some residue—a basis—upon which the unit-characters are imposed? We know, of course, that we cannot isolate this residue from the unit-characters. We cannot conceive a pea, for example, that has no height, no colour, and so on; if all these were removed there would be no living organism left. But while we know that all these characters can be interchanged, we are bound to ask is there something not thus interchangeable? And if so, what is it? We are thus brought to face the further question of the bearing of the Mendelian facts on the nature of Species. The conception of Species, however we may formulate it, can hardly be supposed to attach to allelomorphic or analytical varieties. We may be driven to conceive "Species" as a phenomenon belonging to that "residue" spoken of above, but on the other hand we get a clearer conception of the nature of sterility on crossing.

Though some degree of sterility on crossing is only one of the divers properties which may be associated with Specific difference, the relation of such sterility to Mendelian phenomena must be a subject for most careful inquiry. So far as we yet know, it seems to be an essential condition that in these cases the fertility of the cross-bred should be complete. We know no Mendelian case in which fertility is impaired. We may, perhaps, take this as an indication that the sterility of certain crosses is merely an indication that *they cannot divide up the characters among their gametes.* If the parental characters, however dissimilar, can be split up, the gametes can be formed, and the inability to form gametes may mean that the process of resolution cannot be carried out. In harmony with this suggestion is the well-known experience of hybridisers, that if there is any degree of fertility in the first cross, with subsequent inter-bred generations the fertility may increase.*

Such increase in fertility is generally associated with some greater approximation to one of the parental forms. In terms of our hypothesis, we may conceive this fact as denoting that offspring formed of gametes which have successfully resolved the characters of the heterozygote, and are not bearers of the irresoluble characters, can form their own gametes with less difficulty.

That the sterility of hybrids is generally connected in some way with inability to form germ-cells correctly, especially those of the male, is fairly clear, and there is in some cases actual evidence that this deformity of the pollen grains of hybrids is due to irregularity or imperfection in the processes of division from which they result. It is a common observation that the grains of hybrid pollen are too large or too small, or imperfectly divided from each other.† Such conditions are what we should expect on the hypothesis here suggested.‡

However this may be, it would be of the utmost importance to discover at which of the divisions leading to the production of the gametes, the allelomorphic characters are divided. Correns has pointed out that the evidence of maize proves that in that case the two nuclei of the pollen tube must both be transmitters of the same character, for, in the fruit of the first cross between starch and sugar varieties, those seeds which have sugar endosperms produce pure recessive (sugar) offspring. This fact proves therefore that the nucleus which fertilises the embryo and that which fertilises the endosperm, are transmitters of the same character. Therefore, the separation of the characters does not take place in this case when the two generative nuclei divide from each other.* Further evidence on this question is wholly wanting. Several attempts are being made by others and by ourselves to determine this point by crossing varieties with recognisably different pollens; but, so far, the desired mixture of dissimilar gametes in our cross-bred has not been satisfactorily observed. As soon as some means shall have been found of making visible that differentiation which we now know must exist between the germ-cells of the same heterozygote, a vast field of research will be opened up. Till then, the microscopical appearances accompanying the segregation of the characters must remain unknown, and we are obliged to resort to the cumbrous and protracted method of deduction from the statistical study of the zygotes formed by the union of the several kinds of gametes.

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* Focke, 'Pflanzen Mischlinge,' p. 483; Gärtner, 'Bastarderzeugung,' pp. 333 and 373.

† See *e.g.*, Naudin, 'Nouv. Arch. du Mus.,' 1865, I, p. 95, and Wichura, 'Bastardbefruchtung im Pflanzenreich,' 1865, p. 37. Cases are easy to find.

‡ Remarkable observations bearing directly on this question have recently been published by Guyer ('Science,' vol. 11, 1900, p. 248), as to the spermatogenesis in hybrid Pigeons. The species used are not named, and the account is very brief. He states that in both sterile and fertile hybrids much variation in cell-division was seen, inequalities in chromatin distribution were common and multipolar spindles were abundant. In hybrid spermatogonia there were often more than eight (the normal number) large ring chromosomes. Sometimes there were sixteen small rings. In this case they usually located in two spindles, eight to each. Frequently both large and small rings were present. Guyer suggests, though apparently in ignorance of Mendel's work, that this phenomenon may indicate a "tendency in the chromatin of each parent species to retain its individuality." If so, he points out that in cells with two spindles and eight chromosomes, after division, some of the new cells will have chromatin from one parent and some from the other, and the observed "reversion" of the offspring of hybrids to parent species "may be due to the persistence of the chromatin of only one species in one or both of the germ-cells."

Variation, especially discontinuous variation, of zygotes is in great measure thrown back on that of the gamete. We perceive, in fact, that the production of dissimilar gametes by one zygote may be compared, to take a rough illustration, to a bud-variation, constantly recurring in each heterozygote. Whether the divisions resulting in the formation of the dissimilar gametes are symmetrical or asymmetrical we cannot yet tell; but as in most cases of discontinuous variation, by sufficient searching, occasional instances, particular individuals or strains, will probably be found where the discontinuity is imperfect. As already pointed out also, the existence of exceptional gametes of a mosaic nature must already be inferred. It is unfortunate that so long as the statistical distribution of the zygotes is the only criterion by which the nature of the gametes can be deduced, even cases of impurity in extracted recessives—the readiest form in which imperfect differentiation will be seen—will not suffice to show whether there has been in fact such imperfect differentiation, or only defective dominance.

Mendel's discovery, it will be understood, applies only to the manner of transmission of a character already existing. It makes no suggestion as to the manner in which such a character came into existence. The facts, however, leave no room for doubt that at least one character of each pair of simple allelomorphs has arisen discontinuously. The fact that the gametes of the cross transmit each member of the pair pure, is as strong an indication as can be desired of the discontinuity between them. From imperfection of the records, however, we cannot point to many cases where we know both that the origin was sudden, and that the characters obey Mendel's law, though no one practically acquainted with these subjects will feel any doubt that if those records were complete, there would be abundant evidence to this effect. A positive example, however, is that of *Chelidonium majus laciniatum*, of which the modern origin is recorded,* and the allelomorphic nature was proved by de Vries.† It is scarcely doubtful that such varieties repeatedly arise. The Cupid Sweet Pea is another (p. 140).

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* Correns inclines to the view (based on the fact that pollen grains of crosses between forms of *Epilobium* differing in pollen colour do not show a mixture of the two parental colours) that the separation of characters does not take place when the pollen-grains divide from each other, but when the generative nucleus separates from the vegetative nucleus. Such an observation is, however, surely inconclusive. The pollen-grain is not the germ-cell, but the carrier of the germ-cell, and in any case there *may* be no universal correlation between the appearance of the pollen-grain and the characters it transmits. From what we know of discontinuous variation, and especially from the analogy of that "dichotomy" of characters seen in various parts of hybrids, we incline to the view that the separation of characters will be found to occur at various divisions in various forms. Information on these phenomena is given especially by Naudin, 'Nouv. Arch. Mus.,' I, 1865, p. 150; Focke, 'Oesterr. bot. Ztschr., 1868, p. 139; Macfarlane, 'Trans. Roy. Soc. Edin.,' 1895, vol. 37, p. 203.

With regard to the compound allelomorphs, it must be determined by further investigation whether they similarly can come into existence in their entirety, or whether they are capable of synthesis. At present, though we can perceive the fact that they are capable of decomposition, we know nothing of the reverse process.

In the cases (p. 142) we have discussed, it is plainly the simple allelomorph that has discontinuously arisen.

While we can hardly doubt that, of each pair of simple allelomorphs, *one* must have come suddenly into existence, we cannot tell whether this fact means that something is *added* to the original organism, or whether, from the first, the appearance of the new character is to be regarded as a *replacement* of the corresponding character. For example, we do not know whether the greenness of the peas is due to an *addition* of something to the whole sum of the yellow pea, or to a *substitution* of something for the yellow character. We may partly understand the physiological nature of the yellowness and the greenness, or to take a clearer case, of the relation of the starch endosperm to the sugar endosperm, but this is as yet no help in elucidating the question. If it shall appear that the process is one of addition, the conception of the characters *splitting* may prove an incorrect one, and some other metaphor must be substituted.

Of special importance in this regard will be the study of cases where three or more characters are capable of mutual replacement. All cases studied so far are examples in which the allelomorphs are in *pairs*, but we know instances where three or more alternative forms of the organism occur, and an investigation of such cases may throw light on this part of the problem.

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* For literature see Korschinsky, Heterogenesis, trans., 'Flora,' Ergänzungsheft, vol. 89, 1901, p. 248.

† 'Ber. deut. Bot. Ges.,' 1900, p. 87.

Attention of those who propose to experiment in this direction must, however, be called to the fact that so long as we are dealing with simple allelomorphs, though there may conceivably be more than two forms of gamete (apart from "mosaics," &c.), in respect of each group of simple allelomorphs, yet each zygote can, variation apart, bear two only. Consequently, no zygote can be formed by the sexual process which shall be capable of bearing more than two forms of gamete of each sex. But it is not inconceivable that by grafting or some other form of union, a combination of three or more allelomorphs in one organism may be brought about.

Non-Mendelian Cases.—In the case of Matthiola and among the poultry, instances have been apparently found of definite departure from Mendel's law (pp. 81–6 and 107). It is certain that these exceptions at all events indicate the existence of other principles which we cannot yet formulate. But besides these cases there are three distinct classes of phenomena met with in breeding to which the Mendelian principles cannot be readily applied. It will be useful to consider briefly how each case departs from these principles, and whether by any modification they can be extended to such cases.

Such phenomena are—

1. The ordinary blended inheritance of continuous variations.
2. Cases in which the form resulting from the first cross breeds true.
3. The "false hybrids" of Millardet.

1. *Blended Inheritance.*—At first sight it seems that cases of continuous variations, blending in their hereditary transmission, form a class apart from those to which Mendel's principles apply. But, though it may well be so, the question cannot be so easily disposed of. The essence of the Mendelian conception is, as we have seen, that each gamete may transmit one allelomorph pure. So long as each heterozygote can only exhibit *one* allelomorphic character, the dominant, we can from a study of the heterozygotes and their offspring demonstrate the purity of the gametes. But dominance is a distinct and subordinate phenomenon. We readily perceive that the heterozygotes may show either of the parental characters discontinuously, or various blends between them, while the gametes which composed the heterozygotes may still be pure in respect of the parental characters. The degree of blending in the heterozygote has nothing to do with the purity of the gametes.

It must be recognised that in, for example, the stature of a civilised race of man, a typically continuous character, there must certainly be on any hypothesis more than one pair of possible allelomorphs. There may be many such pairs, but we have no certainty that the number of such pairs and consequently of the different kinds of gametes are altogether *unlimited* even in regard to stature. If there were even so few as, say, four or five pairs of possible allelomorphs, the various homo- and hetero-zygous combinations might, on seriation, give so near an approach to a continuous curve, that the purity of the elements would be unsuspected, and their detection practically impossible. Especially would this be the case in a character like stature, which is undoubtedly very sensitive to environmental accidents.

It is, of course, quite possible that the gametes in such cases do in fact vary as continuously as we see the zygotes do, but this cannot yet be affirmed. The great theoretical significance of this question should therefore lead us to suspend judgment for the present.

2. *First Crosses Breeding True.*—With respect to this phenomenon no experiments on a large scale have yet been made. Most examples are recorded in the form that A and B were crossed together and produced a third form, C. The C's were then bred together and some C's were again produced. We hardly ever are told that in this generation *only C's* were produced. Generally, however, we do not even know so much. The cases for example given by Darwin,* are for the most part general statements that certain new and now definite forms, the Swede turnip, for instance, were produced by crossing. Any such case may, therefore, be merely one of the resolution of compound allelomorphs followed by selection of the forms produced by the union of similar component allelomorphs. This, indeed, is probably the true account of most permanent forms produced by crossing.†

There remain, however, a few cases of which Mendel's‡ own crosses among Hieracia are a good example, in which a distinct form, produced by the first cross, has proved able to transmit its characters to its offspring. Of such cases we know very little. We may, perhaps, notice two features as apparently characteristic of these cases. First, that the results of the first cross may show no uniformity; secondly, that there is often a considerable degree of sterility.

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* 'An. and Plts.,' ed. 2, vol. 2, pp. 73–77.

† We cannot avoid expressing a doubt whether the wonderful series of "mutations" which de Vries has lately recorded ('Die Mutationstheorie,' 1901) as arising from *Œnothera Lamarckiana* do not fall under suspicion that they may owe their origin to some unsuspected original cross. Nothing can take away the extraordinary interest which attaches to these experiments, but until it has been shown in the clearest way that the *Lamarckiana* which gave rise to the "mutants" is a genuine uncrossed form we must feel hesitation in accepting the conclusion which de Vries has drawn from the facts.

This possibility is strengthened by the fact which Professor de Vries has told us, that the pollen of his *Lamarckiana* contains deformed grains, a point which is also mentioned by Pohl (' Oesterr. Bot. Ztschr., 1895, vol. 45, p. 212) in a paper to which de Vries refers (*loc. cit.*, p. 153).

On the other hand, we can scarcely suppose crossing to be the only cause determining the production of heterogeneous gametes, or in other words, variation in sexual descent.

‡ Mendel, 'Abh. Ver. Brünn.,' vol. 8, 1869. See also Swingle and Webber, 'Year-book Dept. Agric.,' 1897, p. 393.

In Correns' terminology such crosses are "homodynamous" and "homoögonous." De Vries speaks of them as "*erbungleich.*" In these instances the new form is able to give off gametes, male and female, carrying its own new character. Such facts plainly indicate a degree of complexity higher than that to which the Mendelian principles can apply, and for the present we have no insight into their nature.

3. *Millardet's "False Hybrids."*—Some allusion must be made to the remarkable results described by Millardet,* which have been the subject of frequent discussion among practical evolutionists. Put briefly, Millardet found that when certain varieties, especially of strawberry, are crossed together, (1) the cross-breds may precisely reproduce the maternal type, without any indication of the paternal characters; (2) in other cases the cross-bred individuals may show *either* the maternal characters pure (save in one case the colour of fruits) *or* the paternal characters pure. Seeds from plants thus exclusively reproducing one parental type themselves gave plants again exclusively of that type. To such forms he gives the name "*faux hybrides*" or "*hybrides sans croisement.*"

In order to estimate the significance of these facts we ought to know of what variations the pure forms are capable, when bred *inter se*, without crossing. Upon this point we have as yet no evidence. If we assume that each of the forms used would, if bred pure, transmit its characters regularly to its offspring, then we should have established that the heterozygote produced exclusively gametes, transmitting the character which appeared as "dominant" in itself, and a new order of facts is thus revealed. It is difficult to see any escape from this conclusion, but, on the other hand, if it could be shown that the pure-bred offspring of the one form could themselves exhibit the characters of the other parent used in the cross, we should recognise that the parent forms themselves produced mixed gametes, and in such a case we should expect that when similar gametes meet in fertilisation the offspring resulting would breed true. On the whole this explanation is very improbable, but as yet it is not wholly excluded in some of the cases in which Millardet's phenomenon is alleged to have occurred.

In our experiments with Matthiola, cases were described which, it can scarcely be doubted, are fully proven. The same is true of some of de Vries' instances,† notably that of *Œnothera Lamarckiana* crossed with the *cruciata* var. of *biennis*. Possible instances occurred in regard to the combs of poultry (p. 122), though, as there pointed out, a simpler explanation is not altogether excluded in those examples. Such phenomena may perhaps be regarded as fulfilling the conception of Strasburger and Boveri, that fertilisation may consist of two distinct operations, the stimulus to development and the union of characters in the zygote.

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* 'Mém. Soc. Sci. Bordeaux,' sér. iv, vol. 4, p. 347.

† 'Ber. deut. Bot. Ges.,' 1900, vol. 18, p. 441.

[Note, added March, 1902.

Several times in the course of these pages, reference has been made to the phenomenon known as the "false hybridism" of Millardet. We are not aware that attempt has yet been made to elucidate that phenomenon. In view of the Mendelian discovery, we think it may not be althogether premature to suggest a possibility, which may perhaps be some guide to further experiment with this phenomenon.

In the false hybrid then, one or more characters are contributed to the zygote by one parent alone, to the exclusion of the corresponding character of the other parent. This exclusive character is exhibited on the development of the zygote; and that the opposite character is really excluded appears from the fact that the offspring of the "false hybrid" do not reproduce the excluded character.

The terms "false hybridism" and "false hybrid," though they have done good service, are clearly inconvenient for the fuller discussion that must arise respecting these facts, and we propose to denote the phenomenon by use of the term *monolepsis*, the ordinary result of fertilisation being distinguished as *amphilepsis*.

It is not yet certain whether monolepsis is a phenomenon peculiar to recessive characters; but while we are fairly sure that some of the cases in which it is seen are instances of recessive characters, we know no certain example of the monoleptic transmission of a dominant character. By the nature of the case, positive evidence of such transmission must be peculiarly difficult to obtain; for the first cross-bred generation would have to be individually tested on a considerable scale by subsequent breeding before such a possibility could be established.

Let us first consider certain features of the process of fertilisation as it may be supposed to occur between gametes bearing similar allelomorphs—for example, an R character. Each gamete bears R, the zygote exhibits it, and the gametes produced by that zygote bear it again.

But we note that we do not *know* whether the character exhibited by such zygote is really the product of the allelomorph of *both* gametes, or is due to the exclusive development of that of one gamete only. Commonly we conceive of all characters of a zygote as the product of both gametes, and in cases of true blended inheritance we must so conceive them. Such a view also accords well with all that we know of the visible processes of fertilisation. Nevertheless, the fact is not certain in the case of the union of similar gametes, and the case may —to take a rough and partially incorrect illustration—be comparable to the known fact that the faculty of speech is, in the normal case, controlled by the centre in the left hemisphere only, the corresponding structures presumed to exist in the right hemisphere not developing or at least not becoming functional. We do not *know*, in fact, whether the character in the zygote depends on, or is in any way affected by, the fact that *both* gametes were bearers of that character.

But if we suppose that the zygote character is thus a product of the two similar allelomorphs in the normal case, we may on that hypothesis form a conception of what may be imagined to take place in the case of monolepsis. For returning to the heterozygote we perceive that on the formation of its gametes there is a resolution or separation of the two dissimilar allelomorphs which came into it at fertilisation. May we not then suppose that in the case of the homozygote a similar separation takes place? The gametes of the heterozygote DR are bearers of D and R respectively separated out of DR; may not the gametes of the homozygote, which are bearers of R and R, receive those allelomorphs by a similar separation occurring between R and R?

If this reasoning prove valid, we suggest the possibility that in the case of false hybridisation the allelomorph is passed on from the zygote to the gamete without such resolution, and that thus it is not in a state which admits of its being affected by the contrary allelomorph of the other gamete. The case may perhaps be compared with the known fact that on separating the two segmentation spheres of an egg, each half may develop into a symmetrical larva.

Unproved as such a suggestion must necessarily be, it is in accord with several of the facts of crossing, of which no other account is as yet forthcoming. If, then, in a cross between D and R, an R be produced in circumstances which leave no doubt that such production is not due to mere environmental disturbance, we must suppose that the D character has never really "*met*" the R character.

Apart from examples of the appearance of a completely recessive form in the first cross, there are curious cases of the appearance of mosaic or pied forms in which the D and R characters form an irregular patchwork. In such a case Correns speaks of the characters as *pœcilodynamous*, a sufficiently expressive term. If, however, it were true that the pied condition is not really due to the dominance failing sometimes and succeeding sometimes, but to the existence in the mosaic of islands of the recessive character in the "paired" or unresolved state, we ought not to describe the phenomenon by reference to dominance at all.

In the introduction to this paper reference was made to the case of Canary—Goldfinch mules. Here the Goldfinch colour is normally dominant. It is said that, generally speaking, 99 per cent. of mules are thus "dark." As was also there stated, the belief is prevalent that in-breeding the hen Canaries has an effect in increasing the proportion of "light"—or canary-like mules. Others have disputed and denied the truth of this belief.

Nevertheless, it is generally admitted that to get "light" mules one should begin with a strain of Canaries which, on mating with the Goldfinch, throw some pied birds. On the hypothesis here suggested, the pied character is supposed to be due to the partially unresolved character of the recessive allelomorph. On in-breeding we may conceive the process of non-resolution on formation of gametes to be carried further. We have seen that cross-breeding leads to the fuller resolution of characters—in-breeding may lead to the contrary result.

With the Canary, as the mule is almost (if not quite) universally sterile, further experiment is impossible, but other cases are available for the experimental testing of this hypothesis.

If it is correct, it should appear that when on crossing a D and R a pied form is produced, showing patches of the R character, then such a pied form on crossing with the dominant again is more likely to give pied recessive or recessive offspring than a pure normal recessive would be, for we are on the hypothesis entitled to believe the gametes of the pied mule to partake of the same character as the zygote itself.

On the older view of breeding such a fact would be paradoxical; for the pied form, inasmuch as it already is part way to the D form, would be supposed *less* likely to show any R in its hybrid than the pure R form.

The fact that Tschermak in his crosses between the pea *Telephone* and yellow varieties obtained a considerable number of seeds greenish or patched with green, is consistent with this view; for this pea, though commonly a green or greenish pea, is liable to great variation, and is frequently mosaic or pied yellow and green.*

The remarkable series of Orchid crosses given by Hurst,† in which the female parent's characters alone appeared as the result of certain extreme crosses, seem rather to illustrate the possibility of parthenogenesis following the stimulus of fertilisation, without zygotic union.]

Galton's Law of Ancestral Heredity in relation to the new Facts.

Such a preliminary survey of the phenomena of heredity as we have attempted would be incomplete without some reference to this subject. We note at once that the Mendelian conception of heredity effected by *pure* gametes representing definite allelomorphs is quite irreconcilable with Galton's conception in which *every* ancestor is brought to account in reckoning the probable constitution of every descendant. With respect of each allelomorphic pair of characters we now see that only four kinds of zygotes can exist, the pure forms of each character, and the two reciprocal heterozygotes. On Galton's view the number of kinds is indefinite.

At first sight it may appear that as the two views are quite incompatible, they must relate to different classes of phenomena. In so far as

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* See Weldon, 'Biometrika,' I, 1902, Pt. II.

† 'J. R. Hort. Soc.,' xxiv, 1900, pp. 104–5.

Galton's law relates to continuous variations, with blended inheritance, this may be the case (see p. 152); but in some of the cases following Galton's rule, notably that of the colour of Basset hounds, the colours dealt with are discontinuous.* Let us consider what evidence there is in this case that the gametes are not pure tricolour *or* non-tricolour, as we should now expect them to be. The first question is, does either colour show dominance? If either were dominant it must clearly be the tricolour, and in view of the fact that both tricolour × tricolour and non-tricolour × non-tricolour are said to have given mixtures, neither colour can be supposed to be exclusively dominant. In this case, therefore, as it is impossible to tell which individuals are pure and which are heterozygotes, Galton's results might possibly have occurred, *and the gametes yet be pure.* More cannot be said without reference to the actual details out of which the tables were constructed.

Attention may also be called to the fact that in cases which fully obey Mendel's ratio (and exhibit dominance), two of the commonest matings happen to give the same result as they would do on Galton's expectation, though the latter is founded on wholly different considerations. Mendel, for instance, expects

DR × DR to give 3Ds and 1R,

and that DR × R will give equal numbers of Ds and Rs. Both these results are, *cæteris paribus*, to be expected on Galton's law, so that it might need a good deal of experiment to distinguish the two classes of cases. A clear distinction would, however, at once be found by comparing the result of DR × R with that of DR × D.

Bearing this in mind, and having regard to the considerations mentioned in the paragraph on blended inheritance, it is impossible to avoid the suggestion that Galton's law may be a representation of particular groups of cases which are in fact Mendelian, in the sense, that is, that there may be purity of gametes in respect of allelomorphic characters. In any case it is now certain that Galton's law cannot be accepted as "universally applicable to bi-sexual descent."

By any practical breeder this must have been always expected, for he knows that while he can rapidly fix some characters, some never come true at all, and others will not come true with any certainty after long selection. The expectation after simple selection is, in fact, quite different for different characters. Mendel's principle disposes of a great part of these difficulties, for we now know that any recessive character may be fixed at once by selecting recessives, and that this fixity may have nothing to do with the novelty of the character, its "prepotency," &c., and that the heterozygote may never come true.

---

* Pearson ('Roy. Soc. Proc.,' vol. 66, 1900, p. 142) has suggested a distinct formula for these cases of alternative inheritance, which he terms the "Law of Reversion." He urges that such phenomena should be treated separately from those of blended inheritance. Both laws alike are of course based on the numerical composition of the ancestry.

Galton's law in fact does not recognise that *absolute* purity which is so common a phenomenon in breeding, as it is in nature. The breeder, in hosts of instances, is not, as a matter of fact, constantly troubled by recurrences of forms with which, even in his own practice, his strain has been crossed. Of this the full explanation is now seen; for if two similar gametes meet, their offspring will be no more likely to show the other allelomorph than if no cross had ever taken place.

CONCLUSION.

We have now sketched the principal deductions already attained by the study of cross-breeding, and we have pointed out some of the results now attainable by that method. The lines on which such experiments can be profitably undertaken are now clear and a wide field of research is open.

The properties of each character in each organism have, as regards heredity and variation to be separately investigated, and, for the present, generalisation in regard to those properties must be foregone. The outlook, in fact, is not very different from that which opened in chemistry when definiteness began to be perceived in the laws of chemical combination. It is reasonable to infer that a science of Stoechiometry will now be created for living things, a science which shall provide an analysis, and an exact determination of their constituents. The units with which that science must deal, we may speak of, for the present, as character-units, the sensible manifestations of physiological units of as yet unknown nature. As the chemist studies the properties of each chemical substance, so must the properties of organisms be studied and their composition determined.

To the solution of the practical problems of heredity, and a determination of the laws of breeding both plants and animals, this is the first step. The attainment of these solutions is now only a question of time and patience.

That the same method will give the key to the nature of specific differences, we may perhaps fairly hope. Certain it is that until the several characters are thus disentangled and their variations classified, no real progress with this question can be expected.*

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* It is absolutely necessary that in work of this description some uniform notation of generations should be adopted. Great confusion is created by the use of merely descriptive terms, such as "first generation," "second generation of hybrids," &c., and it is clear that even to the understanding of the comparatively simple cases with which Mendel dealt, the want of some such system has led to difficulty. In the present paper we have followed the usual modes of expres-

[Since this Report was written, a paper has appeared by Professor Weldon, entitled "Mendel's Laws of Alternative Inheritance in Peas,"* questioning the importance of Mendel's discovery. This paper will be dealt with in a separate publication by W. Bateson, entitled "Mendel's Principles of Heredity," with which is incorporated a translation of Mendel's papers.—March 1902.]

sion, but in future we propose to use a system of notation modelled on that used by Galton in 'Hereditary Genius.' We suggest as a convenient designation for the parental generation the letter P. In crossing, the P generation are the pure forms. The offspring of the first cross are the first filial generation F. Subsequent filial generations may be denoted by F_2, F_3, &c. Similarly, starting from any subject-individual, P_2 is the grandparental, P_3 the great-grandparental generation, and so on. We suggest this terminology here for the consideration of others who are working in the same field. All that is essential is to obtain uniformity, and it is quite likely that a better system may be suggested.

* 'Biometrika,' I, 1902, Pt. II.

[*Note to page* 140, "Cupid Sweet Pea."—Mr. Hurst called our attention to a passage in 'Report of the Sweet Pea Bicentenary Celebration, 1900' (published by Mr. R. Dean), p. 26, where it is stated that Mr. Laxton, of Bedford, crossed Cupids and tall forms, producing almost all *talls* on the first cross. Inquiry from Messrs. Laxton elicited the fact that in this Report the facts were by mistake inverted.]

REPORTS TO THE EVOLUTION COMMITTEE OF THE ROYAL SOCIETY.

REPORT II.

EXPERIMENTAL STUDIES IN THE PHYSIOLOGY OF HEREDITY.

By W. BATESON, M.A., F.R.S., Miss E. R. SAUNDERS, Lecturer, Newnham College, and R. C. PUNNETT, M.A. Fellow of Gonville and Caius College, Cambridge.

EXPERIMENTS WITH POULTRY.

By C. C. HURST, F.L.S.

(Received May 18, 1904.)

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CORRIGENDA IN REPORT I.

Page 24, Table VI. The offspring of S. in. × S. ar. should stand under S. ar, instead of under T. in.
„ 33, note ‡. After "purple" add "on fading."
„ 34. The mark ‡ refers to note § on previous page.
„ 68. In heading for "(R × D)" read "R × D."
„ 71, Exp. 86. "Hoary" column, line 12, for "*br.* 28" read "*br.* 8."
„ 88, par. 5. For "more dingy" read "duller."
„ 104, Exp. 37, and page 105, line 3. For "p. 140" read "p. 96."
„ 105. For "agree precisely, being 3·0 : 1" read "are 2·7 : 1."
„ 111, Exp. 51. For "Legh. 673" read "Legh. 373."
„ 115, Exp. 87. For "those" read "that."

Page 116, line 23. For "even" read "ever."
,, 123, par. 1. For "76 and 77" read "80 and 81."
,, 131. The fanciers' view that the plain-head must be crest-bred is quite correct, because the heavy feathering (and perhaps skull-characters) are needed for a good crest.
,, 140. Mr. E. P. Boys-Smith has given us facts which make it very doubtful if the extension to goats is correct.
,, 160, note on Cupids, line 4. For "talls" read "Cupids."

Professor Weldon ('Biometrika,' II, p. 47) has pointed out that our reference (Rep. I, p. 15, note) to the discovery by de Vries of "a wild specimen" of *Lychnis vespertina* goes beyond the original account. Professor de Vries kindly replied to our questions, that the glabrous plants came from seeds taken from wild plants which were so far withered that their characters were not recognizable. Our expression was therefore incorrect. The other criticisms made by Professor Weldon appear to be based on misapprehensions.

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INTRODUCTION.

This report is a continuation of Report I, 1902. The experiments were distributed as follows:—Those on *Datura*, *Matthiola*, *Salvia*, *Ranunculus* were done by E. R. Saunders; those on *Pisum* by W. Bateson and H. Killby; on Sweet Pea by W. Bateson, E. R. Saunders, and R. C. Punnett; on Poultry by W. Bateson with R. C. Punnett from January, 1904.

The records are only complete to the end of 1903, but reference to the work of 1904 is often necessary.

Part of the expense has been defrayed from funds received from the Government Grant, and we have again to thank the Botanic Garden Syndicate for the free use of an allotment.

Special attention may be called to the illustrations of reversion following heterozygosis, and to consequent complications in the application of Mendelian formulæ. This is best seen in the case of Stocks, where two glabrous types may unite to produce a hoary heterozygote. In another important group of cases the heterozygote may assume either of two reversionary forms, one being a "total," and the other a "half" reversion.

The facts as to Stocks give indications as to the special behaviour of extracted recessives in a complex case, and similar evidence will be provided by the Sweet Peas.

In the poultry the most novel results relate to "Walnut" or Malay combs, where in special cases we meet the phenomenon of *fou* allelomorphs simultaneously segregated, and a definite example of true synthesis occurs.

Disturbances caused by external influences are well exemplified i the seed-characters of Peas, and though of less theoretical significance these facts are valuable as illustrating various sources of error.

"F_1" throughout designates the first filial generation resulting fron a cross. "F_2" means the generation resulting from F_1 and, unles qualified, means the offspring of $F_1 \times F_1$. Other such terms ar urgently needed, *e.g.*, for the various offspring of DR × R, etc., but i seems better to postpone the introduction of further symbols till thei use can be made strictly uniform (see Report I, p. 159, *note*). "P" means an original parent.

DATURA.

In the earlier report reference is made to a result recorded by Godron as following from the cross *D. Stramonium* ♀ × *D. Bertolonii* (= *Stramonium* v. *inermis*) ♂ in which the offspring were all *Bertolonii.* It is there suggested that this statement is possibly the result of an error either in description or experiment, since in all other cases of unions between the armed and unarmed races of *Stramonium* and *Tatula*, however mated, the armed character is dominant.* It so happened that we had not then used this particular union, but the reciprocal cross had been made, and had yielded armed and not unarmed offspring. The cross in question has since been made, and the offspring, 65 in number, were, in accordance with expectation, all armed.† This result confirms the view of Godron's statement expressed above, and shows that the reciprocal unions give identical results.

MATTHIOLA.

The experiments on *Matthiola* described in Report I have been continued, and the following is an account of the further results obtained.

Using a considerable number of types it was found that the inheritance for the most part followed simple Mendelian expectation, but there were certain definite groups of apparently unconformable cases, and also some scattered cases which seemed quite irregular. The investigation of these unconformable cases was a primary object.

In addition an attempt has been made to work out the laws of inheritance of colour, and to investigate the occurrence of double flowers, subjects which were only incidentally studied in the earlier experiments.

I. *The Apparently Unconformable Phenomena.*

A further study of these cases has proved that in many of them the inheritance is on ordinary Mendelian lines, and that the apparent discrepancy was due to the occurrence of an unexpected reversion. The later experiments bearing on these cases are dealt with in four sections numbered α, β, γ, δ.

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* Report I, p. 24.

† This result is beyond question, since these armed cross-breds have now yielded offspring (F_2) showing the expected mixture of armed and unarmed individuals (46 armed, 15 unarmed).—[*Note added December*, 1904.]

(a) *Statement of Results.*

(α) *Experiments in the Form $DR_1 \times R_2$.*

The most interesting cases occurred in this group. The recessive character was glabrousness. From any mating DR × R an equality of D (hoary) and R (glabrous) offspring is the simplest expectation. Nevertheless in certain cases where the second recessive (R_2) differed in flower colour from R_1 used in the first cross, the offspring were *all D, viz., hoary.* The possibility suggested itself that this aberrant result was due to the appearance of a *hoary* heterozygote as the result of the union of two *glabrous* gametes, and, however improbable such a supposition might be, it was not, as we pointed out,* yet excluded. Further experiment has shown that this is the true account. So long as R_1 and R_2 both belong to one of the sap-coloured types—red, flesh,† purple, claret, copper, etc., $DR_1 \times R_2$ gives the usual equality of D and R; but if one of these is sap-coloured and the other white or cream, or if the pair are white and cream respectively, $DR_1 \times R_2$ gives all hoary. (Report I, Table X).‡

Experiment I.—Of the new experiments in the form $DR_1 \times R_2$§ the following three gave a simple Mendelian result.

	Colours of recessives.	Offspring Hoary.	 Glabrous.
1.	Red (br.)‖ R_1 and flesh (br.) R_2	57	54
2.	,, ,, purple (gr.) R_2	32	22
3.	,, ,, claret (gr.) ,,	16	13
		105	89

The following six operations of the same kind representing as many different combinations of colours yielded 1105 offspring, of which *all except three were hoary.*

---

* Report I, p. 86.

† *Flesh* is used here throughout for *pinkish-white* of the earlier experiments.

‡ In some experiments (*e.g.*, 87 and 88) an occasional recessive appeared, but these, in all probability, are due to accidental fertilisation.

§ In the previous Report (p. 10, note) attention is called to the fact that in the earlier experiments the breedings of cross-breds with pure types were almost all in the form of cross-bred ♀ × pure ♂. The proof of the differentiation of the germ cells of the cross-bred therefore rested almost entirely upon evidence drawn from the ovules. In order that the presumed differentiation of the ♂ germ cells should be similarly tested, the cross-breds in the present experiments were also used as pollen parents. In accordance with expectation the reciprocal unions yielded identical results.

‖ The letters in brackets refer to the colours of the seeds; br. = brown, gr. = green.

		Offspring.	
	Colours of recessives.	Hoary.	Glabrous.
4.	Cream (br.) R_1 and white (br.) R_2	315	1
5.	Red (br.) ,, ,, ,, ...	124	1
6.	,, ,, cream ,, ...	234	—
7.	Cream (br.) ,, flesh ,, ...	367	1
8.	,, ,, purple (gr.) R_2	31	—
9.	,, ,, claret ,, ...	31	—

The three glabrous which came from these matings were in all probability due to accidental fertilisation.

Seed colour alone gives no real indication of the behaviour of the recessives in these operations; for combinations in which the two recessives are brown-seeded occur in both groups (1, 4—7), as also do cases (2, 3, 8, 9) in which one recessive has green seeds and the other brown. The departure from the expected mixture of glabrous and hoary is always associated with the meeting either of a sap-coloured form with a white or a cream, or of white and cream with one another.

(β) *Experiments in the form* $DR_1 \times DR_2$.

Experiment 2.—Using cross-breds containing the same D (white *incana*), but different recessives, similar results were obtained.

(1) When R_1 was red and R_2 cream the offspring were 141 hoary.
(2) ,, cream ,, flesh ,, ,, 199 ,,
(3) ,, red ,, flesh ,, ,, 157 ,, and
52 glabrous.

Here, again, the exceptional result followed in those cases where cream was introduced, and a precise Mendelian result when both recessives belonged to the sap-coloured group. In all three cases alike the cross-breds were producing gametes carrying glabrousness, as shown by the results of self-fertilisation (pp. 16—18).

(γ) *Experiments in Crossing Two Glabrous Types,* $R_1 \times R_2$.

At the time of publication of the previous Report no crosses had been made between the various recessive types, nor could any information be obtained in support of the suggestion then tentatively put forward, viz., that a hoary form might be produced by the union of two dissimilar glabrous types.* A large number of such crosses have now been made, and the results are recorded in the accompanying Table.

---

* Report I, p. 86.

Table 1.—Results obtained from Unions between Glabrous Types of dissimilar Flower Colour.

These types were "wallflower-leaved" Ten-week Stocks, of which a collection was very kindly presented to us by Messrs. Haage and Schmidt, of Erfürt. To avoid confusion we have usually retained the descriptive terms used in the earlier Report to designate the various colours. The corresponding terms in Haage and Schmidt's catalogue are as follows:—

Cream = schwefelgelb H. and S.
Red = carmoisin ,,
Light purple = hellblau ,,
Very light purple = lasurblau ,,
Dark purple = dunkelblau ,,

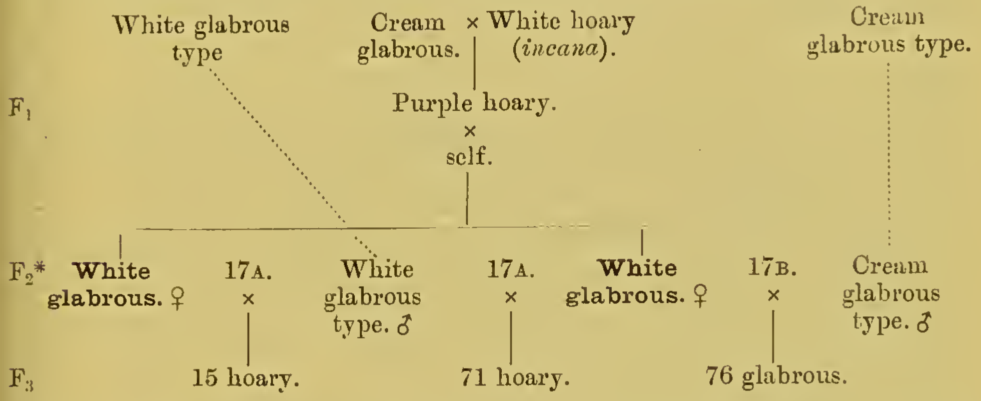
Number of experiment.	Colour of glabrous parents.	Number of offspring.		Colour of offspring.
		Hoary.	Glabrous.	
3	White × cream and reciprocal ..	62	—	Purple.
4	White × red and reciprocal	43	—	,,
5	White × flesh	56	—	,, (paler).
6	White × copper................	11	—	,,
7A	White × dark purple and reciprocal	32	—	,,
7B	Very light purple × white......	38	—	,, (paler).
8	Cream × red and reciprocal	88	—	Red.
9	Cream × flesh ,, ...	46	—	Rose.
10	Cream × copper ,, ...	25	—	Red.
11A	Dark purple × cream	31	—	Purple.
11B	Cream × light purple	22	—	,,
11C	Very light purple × cream......	3	—	,, (paler).
12	Flesh × dark purple	—	30	,, ,,
13	Flesh × copper and reciprocal...	—	32	Rose.
14	Flesh × red	—	27	,,
15	Red × dark purple and reciprocal	—	76	Purple.
16	Dark purple × light purple.....	—	33	,, (paler).

These results are perfectly concordant among themselves, and in complete harmony with those given under (α) and (β), to which they furnish the desired clue. For it appears that *when glabrous types of dissimilar flower colour are crossed together, the resulting offspring are all hoary or all glabrous, according to the particular combination of types employed.* When glabrous white and glabrous cream are crossed with each other or, so far as experiment has yet gone, with glabrous plants of any other colour, the offspring are *all hoary*, thus affording another example of the assumption of an atavistic character by a heterozygote.

This example, it may be noted, illustrates the rarer case of reversion in a structural character, most of those at present known being cases of reversion in colour. When the cross is between glabrous types, neither being white or cream, and both having the cell sap of some shade of red or purple, the offspring are *all glabrous.*

δ. *Extracted R × pure-bred R.*

Experiment 17.—The parentage of the individuals employed in these unions is most easily shown by the following diagram:—



In one case (Experiment 17A) two "extracted" glabrous whites were crossed with a pure-bred glabrous white; *the* 86 *offspring* (*purple*) *were all hoary.* As stated in the earlier Report the F_2 generation in which the glabrous seed-parents came contained the expected number of recessives (roughly 1 in 4).† Such recessives are of two colours only, white and cream (see p. 18), and the numbers—48 white, 15 cream—suggest that possibly the whites may be of two kinds, the one pure, the other containing cream as a recessive.

[Note, added December, 1904.

This prediction has since been verified. Offspring were raised from 13 such extracted F_2 whites. Ten of these individuals bred pure, yielding altogether 106 whites, but no creams; the three remaining plants, among which was one of the two employed in Experiment 17, each yielded a mixture of whites and creams. Hence union of the white- and cream-bearing gametes of the cross-bred (F_1) evidently results in dominance of white, whereas in the case of pure-breds we had reversion to purple.]

Since all the F_3 individuals (86) were hoary, and since we must suppose that in any case some of the gametes of such "extracted" F_2 whites carry white only, it is evident that reversion to the hoary type may result even when the uniting gametes carry the same colour and surface character. The same deduction follows from the observations given under Experiment 2 (1) and (2), where both DR parents were giving off white glabrous gametes, as self-fertilisation proved (pp. 16—18).

---

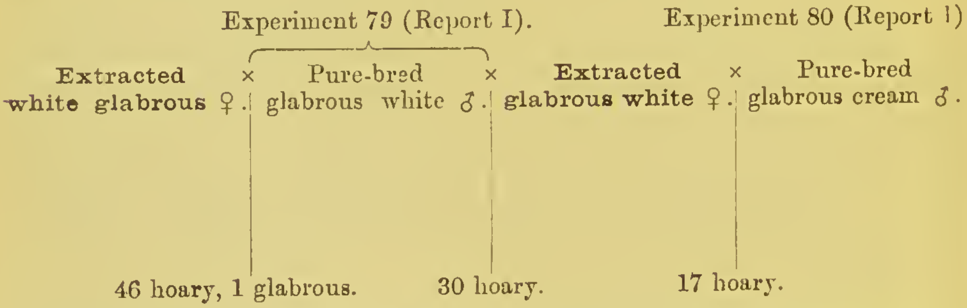
* The coloured members of this family are here omitted.

† Rep. 1, p. 69, Experiment 93.

In Experiment 17B the glabrous white seed-parent—one of the two used in Experiment 17A [and proved later to contain cream as a recessive, see dated note, p. 9] was crossed with a pure-bred, glabrous cream; *the offspring*, 76 *in number*, *were all glabrous*, and either white or cream in colour. Here, although the two recessive parents were coloured respectively white and cream, reversion to hoariness did not occur.

These two results throw a new light upon two somewhat similar experiments recorded in Report I (Experiments 79 and 80), and then regarded as puzzling and unexplained exceptions. In these two cases also the seed-parents were "extracted" glabrous whites. Their parentage was as follows:—An annual hoary white was crossed with a red recessive; one of the resulting hoary cross-breds was then mated with a white recessive. The F_2 generation so bred, though for the most part hoary, contained a few recessives. A knowledge of the results obtained from such matings when *incana* is used as the hoary type, leads us to expect that such an F_2 generation would be *all* hoary, and in consequence to ask whether the above-mentioned recessives can have occurred as the result of accidental self-fertilisation. The total number of these recessives (9)* is large to attribute to an unnoticed source of error, nevertheless until a repetition of the experiments with an annual hoary has disproved this possibility, it must be admitted that such an explanation brings all four experiments most readily into line.

The further operations with two of these "extracted" recessives are shown below:—


Experiment 79 (Report I).
Experiment 80 (Report I)
Extracted white glabrous ♀.
×
Pure-bred glabrous white ♂.
×
Extracted glabrous white ♀.
×
Pure-bred glabrous cream ♂.
46 hoary, 1 glabrous.
30 hoary.
17 hoary.

The diagram shows that with one exception (due in all likelihood to accident) the offspring of the matings between the "extracted" and the pure-bred recessives were all hoary. Here we have reversion not only when the "extracted" white is bred with a pure white (as in

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* Report I, Experiment 63.

Experiment 17A), but also when it is bred with a pure cream (unlike Experiment 17B). *Taken together these results indicate that when an "extracted" white recessive is mated with a pure-bred recessive, which itself is either white or cream, reversion will occur in the succeeding generation provided that the pure-bred recessive does not belong to the recessive type introduced in the original cross.* The result is not affected if the pure-bred recessive and the extracted recessive are both similar in colour.

(*b*) *Conclusions.*

From what has been stated above in α, β, γ, it is clear that this diversity of result occurring alike in the operations $R_1 \times R_2$, $DR_1 \times R_2$, and $DR_1 \times DR_2$ is referable to the same complication. It appears that unions between two gametes carrying the recessive character glabrousness, in conjunction in the one with white or cream colour, and in the other with any colour except that of the gamete with which it unites, whether both are borne by pure-breds (γ), both by cross-breds (β), or one by a pure-bred and one by a cross-bred (α), produce reversionary (hoary) offspring. Whether this principle will be found to hold when similar unions are made between recessives, *both of which are "extracted,"* has yet to be determined. Conceivably the result may vary according as the recessives are "extracted" from cross-breds of like or unlike composition as has already been shown to be the case in δ, where the matings were between an "extracted" and a pure-bred recessive. So far only the albinos among the "extracted" recessives have been employed. In these cases reversion did not occur when the newly-introduced pure-bred recessive belonged to the same type as the recessive grandparent of the "extracted" albino. But when this was not the case, the F_3 offspring reverted to the hoary type. The evidence, in fact, indicates that given a recessive albino, extracted from a DR cross-bred, we require to know the colour of the R grandparent before we can predict the surface character of the offspring obtained by mating it with a pure-bred recessive. Further, it becomes clear that a difference of colour is not a necessary condition of reversion in all cases where two recessives are bred together; under certain circumstances, reversion to the dominant (hoary) form may occur when the recessives are alike in colour.

[Note, added December, 1904.

II. *Further Experiments with Recessives.*

(*a*) *Posterity of R_1R_2 Cross-breds.*

Offspring from these cross-breds were raised (α) by self-fertilisation; (β) by crossing back with R_1 or R_2; (γ) by a cross with R_3; (δ) by crossing with an R_2R_3 cross-bred.

(α) $R_1R_2 \times$ *Self.*

In every case where R_1R_2 was hoary (D), *i.e.*, in every case where F_1 had a white or cream parent, *F_2 was mixed hoary (D) and glabrous (R)*. Though one might have anticipated equality of D and R, the actual result showed a constant excess of D. The numbers obtained in each case were as follows :—

Number of experiment.	Parents.	F_1.	F_2.	
			Hoary.	Glabrous.
18A	Cream R × white R................	All hoary	85	61
	Reciprocal	,,	43	34
18B	Cream R × red R..................	,,	154	88
	Reciprocal	,,	4	2
18C	Cream R × flesh R.	,,	27	16
	Reciprocal.	,,	35	28
18D	Cream R × light purple R	,,	64	51
18E	Dark purple R × cream R.......... .	,,	64	33
18F	White R × red R..................	,,	50	31
18G	White R × flesh R................	,,	34	19
18H	White R × copper R	,,	41	28
18K	Dark purple R × white R...........	,,	44	25

This preponderance of hoary individuals can scarcely be accidental. In 18A and 18B the results indicate a certain amount of association or linking together of surface character with flower colour, the hoary character only appearing in conjunction with sap colours, the glabrous character only with white or cream. How far this complication may account for the irregular result is at present uncertain, since in other colour combinations the glabrous F_2 plants exhibit the same range of sap colours as the hoary, with white, or white and cream in addition. (For details of flower colour see p. 27.) No similar association of seed colour with surface character was apparent. Further consideration of these results is postponed until the evidence from F_3 is available.

In those cases, on the other hand, where R_1R_2 was glabrous, *i.e.*, where both parents had been sap-coloured recessives, *F_2 was all glabrous.* One hundred and ten individuals were thus raised from various colour unions as shown below, and the results accord with simple Mendelian expectation :—

Number of experiment.	Parents.	F_1.	F_2.	
			Hoary.	Glabrous.
19A	Flesh R × red R	All glabrous.	—	5
19B	Copper R × flesh R	,,	—	25
19C	Flesh R × dark purple R	,,	—	32
19D	Dark purple R × red R...........	,,	—	25
19E	Dark purple R × light purple R ...	,,	—	23

(β). *$R_1R_2 \times R_1$ and $R_1R_2 \times R_2$ when R_1R_2 is hoary, and either R_1 or R_2 is sap-coloured, the other being non-sap-coloured.*

$R_1R_2 \times R_1$ or $\times R_2$.

Sap-coloured R employed in both unions.

Number of experiment.	Colours of R types.	F_2.	
		Hoary.	Glabrous.
20A	(White × red) × red	21	14
20B	(White × flesh) × flesh..	26	33
20C	(Cream × red) × red .	14	8
20D	(Cream × flesh) × flesh..	11	8
20E	(Dark purple × cream) × dark purple	6	18
	Total	78	81

Non-sap-coloured R employed in both unions.

Number of experiment.	Colours of R types.	F_2.	
		Hoary.	Glabrous.
21A	(White × red) × white..	11	11
21B	(White × flesh) × white.	10	9
21C	(Cream × red) × cream .	5	12
21D	(Cream × flesh) × cream	8	9
21E	(Dark purple × cream) × cream	10	14
	Total	44	55

In each pair of unions the same cross-bred was mated with R_1 and with R_2. A comparison of the numbers obtained in the separate matings suggests that the discrepancies are probably fortuitous, and do not indicate a real divergence from the simple expectation of equality of D and R. Adding together the results in each group of unions, we get the ratio 1 D : 1·03 R in the case of a cross back with the sap-coloured recessive, and 1 D : 1·25 R when the non-sap-coloured form was the one used in both crosses.

In the case of a repeated cross with white (Experiments 21A and 21B), there was a definite association of surface character with seed colour. The seeds were mixed green and brown. Green seeds gave rise to hoary, brown seeds to glabrous plants. This was not the case in the repeated crosses with cream where the seeds were either all-brown (Experiments 21C and 21D), or of more than two colours (Experiment 21E, where intermediates occurred). In the repeated crosses with sap colours, green seeds and brown seeds each yielded both surface characters.

(γ) $R_1R_2 \times R_3$ *where* R_1R_2 *is Hoary.*

The results in this case were also in agreement with expectation. When R_3 has coloured sap, F_2 *is mixed*, hoary and glabrous, in proportions approaching equality; when R_3 has uncoloured sap, F_2 *is all hoary.*

$R_1R_2 \times R_3$.

R_3 having coloured Sap. R_3 having colourless Sap.

Number of experiment.	Colours of R.	F_2.		Number of experiment.	Colours of R.	F_2.	
		Hoary.	Glabrous.			Hoary.	Glabrous.
22	(White × red) × copper	12	15	26A	(White × red) × cream..	24	—
23	(White × red) × claret..	3	4	26B	(White × flesh) × cream	31	—
24	(White × flesh) × red ...	13	20	26C	(Cream × flesh) × white	24	—
25	(Cream × flesh) × copper	9	7				

(δ) $R_1R_2 \times R_2R_3$ *where* R_1 *alone has Colourless Sap.*

Experiment 27.—The only mating of this kind was in the form (white R × red R) × (dark purple R × red R). F_2 showed the expected equality of D and R (20 hoary, 19 glabrous).

(*b*) *Conclusions.*

The results of breeding R_1R_2 cross-breds with any of the recessives R_1, R_2, R_3, or with a glabrous R_2R_3, are all in accord. In F_2, as in F_1, there is a sharp distinction between the results obtained from sap-coloured and non-sap-coloured forms. We can obtain at will an F_2 which is all hoary, or all glabrous, or hoary and glabrous mixed in approximately equal numbers, by employing recessives belonging to the appropriate group.]

III. *Colour Inheritance.*

The investigation of the laws determining colour inheritance present greater difficulties. Apart from the fact that with a larger number of categories the total number of observations is usually smaller (since it is hardly possible to preserve every individual to maturity), the discrimination of colour is rendered difficult, owing in part to the gradation of shades which the corolla exhibits between unfolding and fading, and in part to the almost universal occurrence of "flaking." These two causes are likely to affect one's judgment of plants seen *en masse;* on the other hand, a difference of shade is less easy to detect when single flowers of individuals are compared.

Some account of the colours observed in various unions appears in the earlier Report; but in those experiments the investigation of colour was not the primary object. Only a relatively small number of plants were flowered. The records, therefore, give no indication of the proportion, and but little of the range of colours occurring in the second (F_2) and later generations. In the present case the investigation was confined to experiments with a small number of authentic types. The white flowered form of *incana* was used as the dominant parent; the recessives were Ten-week Stocks with flowers white, cream, purple, or some shade of red. *Incana* was also mated with another dominant white strain (a hoary white Brompton Stock).

(*a*) *Colour of* F_1 *Cross-breds.*

When any of the above-mentioned recessives was bred with white *incana*, the hoary F_1 cross-breds were all purple.* No difference in colour could be detected between the cross-bred plants which had a white, cream, or red recessive parent. *All resembled the purple-flowered type form of* incana. The cross-breds from the flesh-coloured recessive were of a somewhat paler tint, but fading flowers were as deeply coloured as those recently opened on the other cross-breds. This difference of tint distinguishing the plants produced from the cross *incana* × flesh-coloured recessive is also apparent when a flesh-coloured recessive is bred with a recessive of another colour (Table I, p. 8). Here, flesh-colour × white gave a purple paler than that produced when white was crossed with cream, purple, red, or copper-coloured forms; again, flesh-colour crossed with cream, red, or copper colour, gave rose, whereas cream with red or copper gave a full red.

The colours of the R_1R_2 cross-breds is given in full in Table I (p. 8).

The results may be summarised as follows:—

1. Purple in any combination yields a purple (Experiments 7, 11, 12, 15, 16).

2. Combinations of reddish colours give some shade of red (Experiments 13, 14).

3. All combinations in which white was bred with non-white, give

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* Report I, p. 46, Table.

purple, the heterozygotes being all hoary. In Experiment 7 the significance of the purple is not clear, since purple is introduced in the cross, but in Experiments 3 to 6 it is evident that we have reversion in colour, as well as in surface character.

4. When cream is substituted for white there is again reversion in surface character, but the reversionary purple does not appear (Experiments 8 to 10; Experiment 11 is not in question for the reason given above in the case of Experiment 7).

Cross-breds of the form D_1D_2 were obtained from the mating white *incana* and white Brompton. In this case the parents were similar in surface character and flower colour, but differed in habit. The cross-breds showed no reversion in colour, but were white like both parents.

(*b*) *Colour of Posterity of DR Cross-breds.*

(α) $DR_1 \times$ *Self and* $DR_1 \times R_1$.

Cross-breds from *incana* by a recessive form were self-fertilised, and also crossed back with the original recessive. In each case F_2 exhibited the colours of both parents, and of the cross-breds (F_1); but when cream was used as the recessive there appeared in addition to the cross-bred and parental types at least one new distinct colour form, thus indicating that a resolution had taken place.

The following were the actual numbers recorded:—

Case 1.—*When the Recessive was Red-flowered.*

Number of experiment.	Form of union.	Number and colour of individuals obtained in F_2 from a sample of fruits selected at random.							
		Total hoary.	Total glabrous.	Purple hoary.	White hoary.	Red hoary.	Purple glabrous.	White glabrous.	Red glabrous.
28A	DR × R	102	112	54*	—	48*	59*	—	53*
28B	DR × self	240	56	108	67	43	24	10	10

* The numbers marked with an asterisk are obtained by calculation from the seed colour. Over 700 seeds had been harvested from 13 fruits on 6 individuals; of these 349 were green and 365 intermediate in colour. Each colour gave rise to both hoary and glabrous plants, but all individuals from green seeds were purple-flowered, those from the intermediate seeds red. It is therefore possible to make a prediction as to the colour of those individuals which did not flower, and such glabrous and hoary plants are included in the numbers given above.

The simplest expectation in the case of the cross back with the original recessive is, as regards surface, equal numbers of hoary and glabrous plants: as regards colour, equal numbers of purple and red flowered individuals, the purples arising from the union of a red- with a white-bearing gamete, the reds from the union of two red-bearing gametes; and further, equal distribution of these two colours among the hoary and the glabrous groups. The results obtained fully confirm this supposition. For the expectation in every case being equality, the observed ratio of hoary to glabrous was 1 : 1·09; of red to purple 1 : 1·11; of the four different forms to one another 1·12 : 1·00 : 1·22 : 1·10.

In the case of self-fertilisation we should expect the appearance of six different forms, the three colours, red, purple, and white occurring in conjunction with hoariness and with glabrousness, the ratio of the colours in both cases being as 1 : 2 : 1. An approximation to the theoretical result though less close than in the previous case is clearly indicated. It was noted that the white flowered individuals were of a pure white, but the petals became tinged on fading, a phenomenon not uncommon in the pure-bred white *incana*. Among the red flowered plants there were slight variations in tint, some few individuals showing a bright crimson red, while the great majority were of a more carmine shade.

Case 2.—*When the Recessive was Flesh Coloured.*

Number of experiment.	Form of union.	Number and colour of individuals appearing in F_2							
		Total hoary.	Total glabrous.	Purple hoary.	Rose* hoary.	White hoary.	Purple glabrous.	Rose† glabrous.	White glabrous.
29	DR × self	65	20	15	25	9	3	8	5

Unfortunately no cross back with the original recessive was made in this case, and we have therefore only the rather small totals obtained from self-fertilisation. The results would presumably be the same as in the preceding case, with the substitution of pale shades for the full red and purple. As a fact, the ratio of hoary to glabrous was almost precisely 3 : 1, but the numbers as regards colour are not in accord with expectation. In both the hoary and the glabrous lots there is a preponderance of rose, where we should have anticipated purple, the numbers being such as to suggest that the ratios are, for some unknown reason, reversed. Until further evidence is to hand it must remain doubtful whether the above numbers are too small to give a real indication of the actual ratios, or whether the result is in any way due to a breaking-up, such as seems certainly to occur in the third case described below. It may be noted in passing that were such decomposition to take place, and to result in the production of equal numbers of *two* kinds of pink-carrying gametes, which, meeting with the white gametes showed dominance in the one case and reversion to purple in the other, so that we should represent the proportions of the different gametes formed by the cross-bred as 2 White : 1 Pink A : 1 Pink B, then such reversal of the ratio of purple to pink would be in accordance with expectation, the proportions among both hoary and glabrous lots being 1 White : 2 Pink : 1 Purple. Possibly the appearance of rose instead of a true flesh colour in F_2 may also be accounted for in this way, but until the next generation has been raised the point must remain undecided.

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* The flesh colour of the recessive strain is represented in the F_2 individuals by a rather bluer tint (rose).

Case 3.—*When the Recessive is Cream Coloured.*

Number of experiment.	Form of union.	Number and colour of individuals obtained in F_2 from a sample sowing in Experiment 20*a* and a full sowing in Experiment 20*b*.									
		Total hoary.	Total glabrous.	Purple hoary.	Purple c.e.* hoary.	Red hoary.	Red c.e.* hoary.	White hoary.	Cream hoary.	White glabrous.	Cream glabrous.
30A	DR × R	73	79	14	5	20	11	—	—	33	29
30B	DR × self	324	97	95	7	36	5	32	8	48	15

Both experiments are a repetition of some recorded in the earlier Report (Rep. I, p. 71, Table X, Experiment 86, and p. 74, Table XI, Experiment 93). In the case of *a cross back with the original recessive* ($DR_1 \times R_1$), reference to the earlier experiment shows a simple Mendelian result as regards surface character (297 hoary, 302 glabrous), but an irregular distribution of the three seed colours (green brown, and intermediate), and want of strict association between seed colour and surface character. In the present case the three seed colours were again obtained, and it was noted that the brown and green were respectively uniform in colour, and that the group of intermediates were somewhat graded in tint, the discontinuity between the brown and intermediates being sharper than between the intermediates and the green. No similar observation was recorded in the earlier experiment, and it is conceivable either that the seeds were less well ripened and the colours less well developed, or that the grading of the intermediates was less accurately observed. Be this as it may, the distribution of the seed colours in the present instance was more or less regular, the numbers approximating frequently in individual fruits, as well as in individual plants, to the proportion 1 green : 1 intermediate : 2 brown. Moreover, there was a strict association between seed colour and both surface character and flower colour. A sample sowing of all the seeds from three fruits—about 160—was made, and with one single exception, every seed classed as green or intermediate, gave rise to a hoary, and every brown to a glabrous individual. As regards flower colour every plant derived from a green seed was purple, every one from the intermediate seeds red, and from the brown seeds either white or cream. In the following columns the proportion of the seed colours in each of 23 fruits gathered from 4 individuals is shown, the total numbers are 325 green, 339 intermediate, 651 brown.

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* c.e. = with cream eye; throughout the rest of the petal the plastid colour i obscured by the sap colour.

The inference from the sample sowing is that the total number of seeds would have produced 665 (664 + 1) hoary and 650 (651 − 1) glabrous plants, a sufficiently close approach to the Mendelian ratio 1D : 1R. Of the 73 hoary and 79 glabrous individuals actually obtained from the sowing, 112 have so far flowered; six different colour-forms appeared—purple, purple with cream eye, red, red with cream eye, cream, white. We have then the two parental colours (cream and white), the cross-bred colour (purple), and three other forms. Of these the two with cream eye have the peculiarity that, whereas other coloured forms become more or less streaked with white or "flaked," these show the purple or red streaked or patched with cream; they are, in fact, creams with sap colour added. Although the numbers obtained (see p. 18) are possibly too few to indicate the real proportions of the different forms, they offer several points of considerable interest. It will be noticed that all the glabrous individuals were either white or cream—the parental colours, the purple of the F_1 cross-breds and the novelties seen in the hoary plants were altogether absent; further that the two colours occurred in about equal numbers (29 and 33). Gametes carrying cream colour and glabrousness, and white colour and glabrousness were evidently produced by the cross-bred, and, we must suppose, in equal numbers. Union of the glabrous white gametes of the cross-bred with the glabrous cream gametes of the pure-bred pollen parent results, not in reversion to purple, as occurs when the corre-

Number and Colour of Seeds.

Individual plants.			Individual fruits.		
Green.	Inter.	Brown.	Green.	Inter.	Brown.
110	114	193	16	15	30
			20	24	25
			21	14	27
			13	9	23
			15	22	26
			11	14	36
			14	16	27
48	77	124	16	16	31
			9	21	29
			15	19	31
			5	5	9
			9	16	24
58	62	106	12	21	22
			16	12	19
			15	13	32
			15	16	33
109	86	228	12	16	31
			17	13	42
			14	20	31
			15	10	38
			23	7	37
			18	6	27
			10	14	22
325	339	651			

sponding gametes of two pure-bred types unite (see Table I, Experiment 3), but in dominance of white. We may, in fact, expect that these whites will yield both white and cream plants in F_3, while the creams will breed true and produce only cream.*

[Note, added December, 1904.

This expectation has now been fulfilled. Separate sowings were made from 16 of these extracted whites, *and in every case* F_3 *showed a mixture of whites and creams.* On the other hand *an* F_3 *of creams only was obtained from six* F_2 *creams selected at random.*]

The hoary plants, on the contrary, show a total absence of both white and cream, a fact which indicates that the union of white and cream or even of cream and cream will give different results as regards colour according as the gametes are carrying these colours in conjunction with hoariness or with glabrousness. The appearance of an entirely new colour—red—suggests that a breaking-up of the constituent colours has occurred in the gametogenesis of the cross-bred. The evidence from the seed colours indicates that the red-flowered plants, whether self-coloured or with cream eye, will be equal in number to those with flowers wholly or partly purple, but the proportion of selfs to bicolours in each case is hardly to be gathered from the numbers at present available. We may, therefore, pass to a comparison of these results with those obtained from *self-fertilisation* of the cross-breds (Experiment 30B). Here the grading of the seed-colours was more continuous, and the sorted groups did not exhibit such a strict correlation with surface character and flower colour as to permit of sample sowings. A full sowing yielded the results given above (p. 18). The proportion of hoary to glabrous is almost precisely 3 to 1. The colours of the glabrous plants are similar to those obtained from the cross back with the original recessive, viz., cream and white only; the ratio (almost exact) 3 : 1 suggesting as before that when the glabrous cream- and glabrous white-bearing gametes meet there is again dominance of white.* The hoary individuals exhibit the same colours as when the mating was of the form $DR_1 \times R_1$, and, in addition, white and cream. The last-mentioned form, we may presume, will breed true. From its appearance here we can scarcely doubt that the cross-bred is producing gametes carrying cream colour in conjunction with hoariness. The view that the results of unions of cream with cream will vary according as the gametes are also carrying the hoary or the glabrous character is thus further confirmed. [It will be remembered that when these very cross-breds were mated with a pure-bred glabrous cream, no hoary creams appeared.]

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* That creams can be bred from whites we already know, since it is a well-established fact that certain white strains habitually throw cream "doubles." In the hope of elucidating this and other points connected with the appearance of the cream colour, a histological investigation of the petals is now being made.

Here, as in the preceding case, it is doubtful whether the numbers are sufficiently large to give a reliable indication of the true ratios in the smaller groups of hoary plants. Moreover we do not yet know what forms the bicolours will produce. It must be borne in mind that flower colour in Stocks is due to the presence of colour, either in the cell sap, or in the plastids, or in both; white results from absence of colour in both these cell constituents. We can, therefore, classify these various colour forms under four heads as shown below where the + and − signs indicate presence and absence of colour respectively.

Now the original cross was between plants belonging to i and ii; plastid colour behaves as a recessive character, all individuals in F_1 coming under iii. In F_2 we get the four possible combinations of the sap and plastid characters. In the case of i and ii we may probably

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* The actual proof is furnished in F_3 (see note, p. 9).

Totals in F_2.	i. −Sap. −Plastid.	ii. −Sap. +Plastid.	iii. +Sap. −Plastid.	iv. +Sap. +Plastid.
	White.	Cream.	Self-coloured reds and purples.	Reds and purples with cream eye.
Expt. 30A....	33	29	34	16
,, 30B....	80	23	131	12

accept the ratio 1 : 1 in Experiment 30A (DR × R) and 3 : 1 in 30B (DR × self). In the case of iii and iv the relation is probably less simple, and for elucidation of this point we must await further evidence.

Looking at the colour groups from another point of view, and taking sap colour alone into consideration we may class the selfs and bicolours together; we then have among the hoary individuals in 30B: 102 with purple sap, 41 with red sap, 32 white, 8 cream.

These numbers suggest the ratio 9 : 3 : 3 : 1, which would give 103·5 : 34·5 : 34·5 : 11·5, and though the result departs in some measure from this expectation, it is not impossible that this discrepancy may be fortuitous.

Tschermak,* crossing a white flowered strain of *M. glabra* with a deep blood-red coloured form of *incana* obtained in F_2 a mixed offspring in the proportion of 3 hoary coloured to 1 glabrous white (actual numbers 2249 and 845). The hoary individuals were divisible into four colour groups—pure violet, ash violet, pure rose, ash rose—the numbers indicating the ratio 9 : 3 : 3 : 1. Such a ratio we expect when two pairs of allelomorphic characters exhibit the phenomenon of simple Mendelian dominance, and in the present case this relation was deduced by Tschermak from the numbers he obtained in F_2 and further confirmed by his results in F_3. The pure colours were found to be dominant over the ash tints, the violet shades over the pink. Whether the corresponding ratio in our own experiments will be substantiated, and whether it is the outcome of such a simple Mendelian gametic ratio, can only be decided by further experiment.

Tschermak's observation leads to the important conclusion that certain of the F_2 individuals which exhibit a reversionary colour are homozygous, and will breed true; and, consequently, that in the gametogenesis of F_1, an actual synthesis has taken place. Our own experiments are not yet sufficiently advanced to give a clear indication on this point, though it is scarcely doubtful that the next generation will show this result.

As stated above (p. 21), the red colour obtained in these experiments (30A and 30B) is wholly new, and for the present we can form no certain opinion as to the components which combined to produce it. As possibly bearing upon this point, however, we may recall that on crossing a glabrous cream with a *white-flowered hoary Brompton Stock*, a similar red colour occurs in F_1 (Rep. I, Table, p. 46), a fact which suggests that certain gametes of the *incana* cross-breds, carrying *white* and *cream* respectively, may similarly unite to produce red where one might otherwise have expected reversion to purple.*

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* 'Beihefte z. Bot. Centralb.,' 1903, Heft. 1.

On the other hand, it may be that the *red* of the Brompton cross-breds is analogous with the *purple* of the *incana* cross-breds. The original Brompton Stocks were probably red, and the appearance of red in their crosses may be a reversion to this type just as the purple in the *incana* crosses is a reversion to the purple *incana*.

The following passage from Bradley lends support to this view :—"There are five Sorts of them (*i.e.*, Stocks) besides the Dwarf Kind or Annual Stock for Edgings. The White Flowering Kind, that with the Purple Flower, the strip'd Sort, the large Red Brompton Stock, and that Sort which blossoms the first year; of all which the Brompton Kind is esteem'd to be the best."† Again, Miller‡ gives "*Leucoium incanum majus coccineum*, the Greater Hoary Crimson Stock-July-flower, vulgarly called the Brumpton Stock," and in Loudon§ it appears under the name "*Matthiola coccinea*." It should, however, be noted that the appearance of red is not universal among Brompton cross-breds: though glabrous cream × hoary Brompton white yields red, glabrous white × the same type yields purple, whereas with *incana*, reversion to purple results from matings with any of the recessives employed. (The tint in the case of a flesh-coloured recessive is somewhat paler than in the other crosses.) As regards the origin of the cream form, we can find no precise statement. It was evidently known to Parkinson,‖ who speaks of *Leucoium sativum albido luteum simplex*, and adds "of no great regard, but only for rarity, and diversity from the rest."

(β) $DR_1 \times R_2$

Nine different combinations of recessives were employed in these unions (see pp. 6 and 7, Experiment 1). The colour results were as follows:—

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* For a more obvious case of two reversionary types *cf.* the case of Sweet Peas.

† 'New Improvements of Planting and Gardening, both Philosophical and Practical,' 1718, Ed. 2, pt. 2, p. 143; "Of Stock-July-Flowers."

‡ 'The Gardener's Dictionary,' 1731.

§ 'Encyclopædia of Plants,' 1829, p. 538.

‖ 'Paradisus,' 1629, p. 260.

	Colour of recessives.	Colour of F_2 cross-breds.
1.	Red R_1 and flesh R_2	45* pale purple, 70* rose.
2.	Red R_1 and purple R_2	All purple (54).
3.	Red R_1 and claret R_2	,, (6).
4.	Cream R_1 and white R_2	,, (238).
5.	Red R_1 and white R_2	120 purple, 3 red (? due to self-fertilisation).
6.	Red R_1 and cream R_2	103* purple, 112* red.
7.	Cream R_1 and flesh R_2	109* pale purple, 115* rose.
8.	Cream R_1 and purple R_2	All purple (29).
9.	Cream R_1 and claret R_2	,, (24).

These results may be summarised thus—

(i) When any shade of purple, whether a reddish purple or a true purple, was introduced in the cross as in 2, 3, 8, 9, F_2 was purple; in the cases where a true purple was used (2, 8), it is uncertain whether this colour in F_2 is due to dominance or reversion.

(ii) Reversion to purple occurred in both cases in which a white recessive was used. (In 5 the total included three reds, but these, in all probability, were the result of accidental fertilisation.) When the white was employed in conjunction with cream (4), the F_2 plants varied slightly in tint, but the series of colours which are borne by the gametes of the F_1 cross-breds, and which are manifested on self-fertilisation, vanish under the reversionary influence of the white recessive.

(iii) When cream is used in conjunction with some shade of red (6 and 7), the F_2 generation is mixed, one half only revert to purple, the other half are reddish, light or dark according as the other recessive was full red or flesh-coloured.

(iv) When both recessives were of some shade of red (1), the F_2 generation was again mixed, but the proportion of purple to red appears to be less than in the preceding case.†

(γ) $DR_1 \times DR_2$.

The colour results obtained when cross-breds containing the same dominant (white *incana*) and a different recessive were bred together, *i.e.*, when the experiments were of the form $DR_1 \times DR_2$, were as follows :—

Case 1.—(Red glabrous × white hoary) × (cream glabrous × white hoary). Experiment 31A. One hundred and forty-four seeds were harvested from a single such cross-bred; 108 green, 36 intermediate, or precisely 3 : 1. As previously stated (p. 7), the 141 plants derived from these seeds were *all hoary;* in colour they were either red, purple, or white, the first mentioned being invariably derived from the intermediate seeds, the two latter from the green. The numbers actually obtained were 54 purple, 30 white, 21 red, a result which, taken together with the evidence of the seed colours, indicates the ratio of the three forms as 2 purple : 1 white : 1 red. Conceivably the purples arise from the union of gametes, carrying white and cream or white and red : the reds from a combination of the red and cream elements (compare Experiment 9, Table I): the whites from the union of two white-bearing gametes, being probably homozygous.

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* The numbers marked thus * are calculated from the seed colours after a sample sowing has been made.

† For a similar deficiency of purple in F_2 when a flesh-coloured recessive was used, *cf.* Experiment 29, p. 17.

Case 2.—(Cream glabrous × white hoary) × (flesh glabrous × white hoary). Experiment 31B. The results in this case are precisely analogous with those of the previous experiment, except that white-flowered individuals were obtained from the intermediate as well as from the green seeds, and that the coloured plants were of the paler shade of purple and of red characteristic of unions with the flesh-coloured form. The actual numbers were 50 pale purple, 25 white, 21 rose. Glabrous plants were again absent (see p. 7).

Case 3.—(Red glabrous × white hoary) × (flesh glabrous × white hoary). Experiment 31C. This experiment, it will be remembered, gave the expected proportion 3 hoary to 1 glabrous (see p. 7). The colour results, though less close in the case of the seeds, agree with those of the preceding experiment. There were 169 green seeds and 67 intermediates; both produced white and coloured plants. All three colours—purple, red, and white—appeared among both the hoary and the glabrous plants, the records from those which have already flowered indicating the same proportions as in the two preceding experiments (53 purple, 32 white, 25 red).

A comparison of these three cases discloses a point of considerable interest, but as yet not easy of explanation. All the three kinds of cross-breds employed owned the same father—a white *incana* plant —and all on *self-fertilisation* yielded a definite proportion of glabrous whites. Yet when they are *bred together* in each of the three possible ways *glabrous whites are wanting in two combinations out of the three—in the two in which cream is introduced as one of the recessives.* The mere fact that the uniting cross-breds contain different recessives is not in itself a sufficient explanation of this unexpected result, for in the one case (3) in which glabrous whites were obtained this was equally the case, the one cross-bred containing a flesh-coloured recessive, and the other a red. We can only suppose that the suppression of the glabrous whites is one more of the many peculiar features distinguishing cream from sap-coloured recessives in unions of this form. We appear to have definite evidence that when cream is employed in unions with *incana* resolution or decomposition of the colour allelomorphs occurs, but whether such decomposition is in any way to be considered as the cause of the unexpected result referred to above, we have at present no means of determining.

[Note, added December, 1904.

(c) *Colour of Posterity of R_1R_2 Cross-breds.*

(α) *R_1R_2 × Self.*

(i) When R_1 and R_2 are the non-sap-coloured forms, white and cream (Experiment 18A).

In this case a definite association of the two characters, leaf surface and flower colour, was clearly apparent. As stated above (p. 12), F_2 showed a mixture of D (hoary) and R (glabrous), D being somewhat in excess. None of the glabrous individuals had sap-coloured flowers, all were either white or cream, the parental colours, the numbers (59 white, 16 cream) suggesting here, as elsewhere, the ratio 3 white to 1 cream. The hoary plants invariably had coloured sap; four distinct colour forms appeared, viz., purple, red, a terra-cotta or copper shade, and a livid blue or plum colour. The majority of the sap-coloured plants were self-coloured, but some individuals in each colour group showed the bicolour form with cream eye. One hundred and eighty-eight plants were flowered, the sap colours being distributed as follows:—

	Purple.	Red.	Plum.	Copper.	
Self	49	16	23	6	= 94 + sap − plastid.
Bicolour	9	5	3	2	= 19 + sap + plastid.
Total	58	21	26	8	

The numbers give no certain indication of the gametic formula in regard to flower colour. From seed colour we get no further clue; green seeds yield the blue shades (purple, plum); brown seeds the red shades, and white and cream; intermediates give both reds and blues. In regard to colour, as in the case of surface character, we must await the evidence from F_3.

(ii) When R_1 and R_2 belong respectively to the sap-coloured and the non-sap-coloured groups (Experiments 18B to 18K).

In four of these operations (Experiments 18B to 18E), cream was the non-sap-coloured type, in four others (Experiments 18F to 18K) white was used. In both sets of unions, where the numbers obtained were fairly large, the same range of sap-coloured forms was found in the glabrous as in the hoary plants; where this was not the case, it was evidently due to the smallness of the totals.

The colours crossed with cream were red, flesh, and light and dark purple; thus, the unions were between + sap − plastid and − sap + plastid. In three out of the four matings the sap and plastid characters were redistributed in F_2, and gave all the four possible combinations, viz., + sap − plastid (self sap-colours), + sap + plastid (bicolours), − sap + plastid (cream), − sap − plastid (white). In the fourth case cream has not yet appeared, but it can scarcely be doubted that it would with a larger total. Thus, white may appear in F_2 as the result of crossing, though both parents (P) be coloured. White and cream only occurred in conjunction with glabrousness, but in these unions definite association of surface character with particular colours was limited to these two forms. No clear indication has yet been obtained of the ratios of the various colours, or of the proportion of selfs to bicolours. The following list shows the colour forms obtained in each union :—

Colours of recessive parents.	Colours occurring in F_2.	
	a. Among both hoary and glabrous plants.	*b.* Among glabrous plants only.
Cream and red	Red (self and bicolour).	White and cream.
Cream and flesh	Various reds (self and bicolour.	,, ,,
Cream and light purple	Purple, red, rose (in each case self and bicolour).	,, ,,
Cream and dark purple	Purple (self and bicolour), red (self and bicolour).	White (cream has not yet appeared).

The sap colours used in the unions with white were red, flesh, copper, and dark purple. In these crosses, as in the matings with cream, decomposition of the colour allelomorphs seems to occur, for in every case F_2 showed a variety of sap-coloured forms. Here, also, white is associated with the glabrous character. The colours obtained are given below :—

Colours of recessive parents.	Colours occurring in F_2.	
	a. Probably among both hoary and glabrous plants.	*b.* Only among the glabrous plants.
White and red	Purple, plum, red, copper.	White.
White and flesh	Purple, rose, copper, flesh.	,,
White and copper	Purple, plum, red, copper.	,,
White and dark purple	Purple, plum.	,,

The red colours were always less numerous than the blue, and one or another of these shades was wanting among the recessives in each of the first three combinations. In all probability these forms would appear in a more numerous offspring. At present the numbers are too small to give a reliable indication of the various ratios.

(β) *$R_1R_2 \times R_1$, and $R_1R_2 \times R_2$ where R_1R_2 is hoary, and either R_1 or R_2 is Non-sap-coloured, the other being a Sap-coloured Form.* (Experiments 20 and 21.)

The results of these operations are in harmony with those obtained from self-fertilisation of R_1R_2. A repeated cross with a non-sap-coloured form gave a *mixed* F_2 (sap-coloured and non-sap-coloured); with a sap-coloured form, an F_2 *all sap-coloured;* colourless sap was associated with the glabrous character. When R_1 was white, white was, as we should expect, the only non-sap-coloured form appearing in F_2; when R_1 was cream, both cream and white were obtained. Bicolours only occurred when cream was used in both crosses. The following table shows the results in each case:—

(Experiment 20).

(*Sap*-coloured form employed in both unions.)

Colours of R types.	Colours occurring in F_2.	
	a. When hoary.	*b.* When glabrous.
(White × red) × red	Purple, reds (various).	Purple, reds (various).
(White × flesh) × flesh	Pale purple, lilac, rose, flesh.	Pale purple, lilac, rose, flesh.
(Cream × red) × red	Red.	Red.
(Cream × flesh) × flesh	Rose, flesh.	Rose, flesh.
(Dark purple × cream) × dark purple.	Dark purple.	Dark purple.

(Experiment 21).

(*Non-sap*-coloured form employed in both unions.)

Colours of R types.	Colours occurring in F_2.	
	a. When hoary.	*b.* When glabrous.
(White × red) × white	Purple, plum.	White.
(White × flesh) × white	,,	,,
(Cream × red) × cream	Red bicolour.[1]	White, cream.
(Cream × flesh) × cream	Red bicolour, rose.	,,
(Dark purple × cream) × cream.	Purple,[2] red, red bicolour.	,,

In all probability, one or two additional forms would appear if larger numbers were used, *e.g.*, red, perhaps, at ^{1}, and purple bicolour at ^{2}. It is, however, evident, that in a repeated cross with a non-sap-coloured form, we have the same kind of association as in the case of $R_1R_2 \times$ self. Presence of sap colour is associated with the hoary character, absence of sap colour with glabrousness. When the repeated cross is with the sap-coloured form, we find the same range of sap colours in the glabrous as in the hoary plants.

(γ) $R_1R_2 \times R_3$ *when* R_1R_2 *is Hoary* (*Experiments* 22, *and* 24—26).

The results in six such operations were as follows :—

	Colours of R types.	Colours occurring in F_2.
i.	(White × red) × copper	Purple, red.
	(White × flesh) × red	Purple, various reds.
	(Cream × flesh) × copper.........	Various reds.
ii.	(White × red) × cream	Purple, red.
	(White × flesh) × cream	Purple, various reds.
	(Cream × flesh) × white	Purple.

In all these unions, whether R_3 had coloured sap (as in i), or colourless sap (as in ii), F_2 was all sap coloured. (A single glabrous white, which appeared in one case, must be attributed to accident.) When F_2 showed a mixture of hoary and glabrous plants (i), the same variety of colour occurred in both groups. From the colours obtained in the last two matings, we may conclude that the results which follow from a particular combination of colours, may vary according to the order in which the colours are used.

(δ) $R_1R_2 \times R_2R_3$ (Experiment 27).

The mating (white × red) × (dark purple × red) gave purples and reds, in the ratio 3 : 1, in both the hoary (15 purple, 5 red) and the glabrous (15 purple, 4 red) groups.]

IV. *Frequency of Occurrence of Double Flowers.*

The occurrence of double flowers was recorded in the earlier experiments, but, as only a small percentage of plants were flowered, no statistical evidence of value was obtained on this point. The investigation of flower colour gave a convenient opportunity for fuller observation respecting doubling. Inasmuch as this feature is commonly supposed to depend largely on external conditions, it was not expected that the distribution would exhibit any obvious statistical regularity. Observation, however, has shown that doubling among the offspring of cross-breds may occur in proportions characteristic of ordinary recessives; and there is little doubt that, in some cases, it is related to the single flower as recessive to dominant.

One feature of this case distinguishes it from the others with which we have dealt. In double Stocks the anthers and the pistil are not recognisable, and the centre of the flower is filled by a mass of petals. There is apparently petalody of both male and female organs, accompanied by reduplication or pleiomorphy,* but the precise morphology of the variation does not seem to be wholly clear. For the purpose of this discussion, the important point is that neither pollen nor ovules are present in the double flowers. Our experience agrees with that of almost all who have described this phenomenon in Stocks, that the variation is usually complete, intermediate conditions being only occasionally met with, and no mixture of doubles and singles having ever occurred on any individual plant.

It follows, therefore, that doubles must generally be the offspring of normal singles, and no double ever has a fully double ancestor in the direct line. In a pure race, therefore, the two forms probably constitute a pair of "*Mittel-rassen*," to use de Vries' term. In other words, the singles, though constantly selected, may continue to throw off doubles. Though, as will be immediately shown, the double Stock may behave to the single as a Mendelian recessive, the type individuals, which give off doubles, can scarcely be normal DR, since it is well known that as many as 80 per cent. of doubles, or even more, can sometimes be obtained on self-fertilisation, or fertilisation *inter se*.†

A brief note of the earlier references to doubling in Stocks has some value. From the nature of the case it is fairly certain that this doubling must have arisen in the past, as now, by mutation, and that no gradual selection can have been instrumental in its production. Though the earlier herbals devote much attention to Stocks, none that we have seen mention any double form. The first notice of double Stocks we have found occurs in Dodoens‡ who states that a form of Stock with a multiplicity of leaves in the flower is found in gardens, but it is extremely rare, since it is of the larger sort, flowering in spring, and requiring great care to prevent injury by cold in the winter months. Two years later Lobel and Pena§ give the further information that both Wallflowers and Stocks can be greatly improved by horticultural treatment, and frequent transplantation, becoming double as a Moss rose, but that they are then destitute of seeds. A figure of this double form is introduced by Lobel into his 'Kruydtboeck' (1581), it also occurs in Dodoens ('Pemptades Sex,' 1583), and is again used later by Gerarde and others.

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* See Masters' 'Veg. Terat.,' 1869, especially appendix.

† Horticultural literature abounds with recipes for increasing the output of doubles in Stocks, and though the methods suggested often seem quite opposed to each other, the balance of evidence certainly favours the belief that the variation —viz., the production of gametes bearing this recessive character—may be promoted, if not caused by, environmental disturbance. Until critical experiments have been made, detailed discussion of these various statements is hardly profitable.

‡ 'Florum et coronariarum odoratarumque nonnullarum herbarum historia,' 1568.

§ 'Stirp. adv. nova,' 1570.

The seedlessness of double Stocks is mentioned by many authors of the 16th and 17th centuries (see especially Parkinson*) who all agree that doubles can only be raised from the seed of singles, none ever referring to intermediate states.

Nevertheless Hill† has the following instruction for obtaining double Stocks: "Let him select such single Stocks for Seed as are large, robust, wellgrowing, and would naturally have a vast Multitude of Flowers; and such as have in some Flowers somewhat above the proper Number of Petals, five, six, or more: this is the first Tendency in Nature to Doubleness; and this he should carefully watch for the farther Improvement." One is inclined to regard this advice as based on analogy rather than on practical experience, and of equal value with another method much advocated, the planting of singles in close proximity to doubles. Nevertheless, two writers, apparently independent, in answer to an inquiry in 'The Floricultural Cabinet' (1833, pp. 21, 89, 103) give precisely the same recommendation of gradual selection, and the statement of the writers' experience has every appearance of authenticity.

On the other hand, Chaté,‡ a French horticulturist, in whose family the cultivation of Stocks had been practised for more than 50 years, referring to this method of selection, writes that moderately good results have been obtained by selection of plants as seed bearers which show a fifth petal; that in the first year such plants have yielded 50 to 60 per cent. of doubles, but that in the second year the sowings have only produced a small proportion. His own personal experience, he adds, is that such plants are very rarely met with, and that it would have been impossible to count on them for obtaining a supply of seeds. The German cultivators are said to grow the seed plants in pots, with a minimum of water, thus obtaining 60 to 70 per cent. of doubles, while the French practice of removing the weaker branches, and sowing seed exclusively from the lower parts of the pods, is said to yield as many as 80 per cent. The average yield in the case of sample sowings of seeds from the upper quarter of the siliqua was only 30 to 35 per cent. of doubles, from the remaining lower portion 75 to 80 per cent. were obtained.

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* 'Paradisus,' 1629, p. 261:—"But this you must understand withall, that those plants that beare double flowers, doe beare no seede at all, and is very seldome encreased by slipping or cutting, as the next kinde of double is: but the only way to have double flowers any yeare, (for this kinde dyeth every winter, for the most part, after it hath borne flowers, and seldome is preserved) is to save the seedes of those plantes of this kinde that beare single flowers, for from that seede will rise, some that will beare single, and some double flowers, which cannot bee distinguished one from another, I meane which will be single and which double, untill you see them in flower, or budde at the least. And this is the only way to preserve this kinde: but of the seede of the former kinde was never known any double flowers to arise, and therefore you must be carefull to marke this kinde from the former."

† 'Eden,' p. 567, 1757.

‡ E. Chaté, 'Cult. prat. des Giroflées,' pp. 63, 80.

Our observations are in full agreement with those of Chaté. Flowers with one or two extra petals are occasionally seen. In the present year, some thirty biennials growing in the open survived the winter, and several of these flowering in early spring produced scattered flowers with one or two extra petals. Apart from these, only one or two instances have been observed, though in late autumn poor flowers may occasionally show petals deeply cleft. In fact, doubles at the present day are obtained from normal singles, as recommended by the early writers on horticulture.

The evidence in regard to doubling was furnished by experiments, the results of which, in the case of surface character and flower colour, have already been given in detail. As previously stated, the types employed were the white form of *incana* and glabrous Ten-week Stocks of various colours. The tendency to produce doubles is a characteristic feature of the Ten-week races, which constantly yield singles and doubles mixed. In white *incana*, on the other hand, this phenomenon was never seen, and in the wild plant it probably does not occur.* When the two are bred together in various ways the distribution of doubles was found to exhibit a distinct regularity.

The facts were as follows :—

No doubles occurred in F_1 when *incana* was bred with one of the Ten-week strains (whether D × R or R × D). Among such cross-breds it was not uncommon to find flowers with seven or eight stamens; this, however, is undoubtedly a wholly different phenomenon, and one which may have some interest in regard to the question of the origin of the Cruciferous andrœcium.

In the F_2 generation derived from the above, doubles were also absent when the mating was in the form DR × D, or D × DR.

The results obtained from the operations $DR_1 \times$ self, $DR_1 \times R_1$, $DR_1 \times DR_2$ and $DR_1 \times R_2$ are shown in the accompanying table :—

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* A point of some interest; since it was in the biennial type, according to Dodoens, that doubles were first observed.

Table II, showing Distribution of Doubles in F_2 obtained from the Operations $DR_1 \times$ Self, $DR_1 \times R_1$, $DR_1 \times DR_2$, and $DR_1 \times R_2$.

Number of experiment.	Form of union.	DR individuals used in F_1.	Totals of singles and doubles.		Ratio of singles and doubles.	Analysis of totals.										
						Total hoary.	Total glabrous.	Total purple.	Total red.	Total white.	Purple hoary.	Red hoary.	White hoary.	Purple glabrous.	Red glabrous.	White glabrous.
30B	$DR_1 \times$ self when R_1 is cream	Plants A_1, A_2*	Single	241												
			Double	—												
30A	$DR_1 \times R_1$ when R_1 is cream	,, A_1, A_3, A_8	Single	112												
			Double	—												
31A, 31B	$DR_1 \times DR_2$ when R_1 is cream and R_2 has coloured sap	,, $A_3 \times C_1$ $A_4 \times B_3$	Single	191												
			Double	—												
1 (4)	$DR_1 \times R_2$ when R_1 is cream and R_2 white	,, A_1, A_3, A_4 A_6, A_7	Single	238												
			Double	—												
1 (7), (8), (9)	,, when R_1 is cream and R_2 with coloured sap	,, A_2, A_3, A_5, A_8	Single	277												
			Double	—												
1 (5)	,, when R_1 has coloured sap and R_2 is white	Plant B_4	Single	120												
			Double	—												
1 (6)	,, when R_1 has coloured sap and R_2 is cream	Plants B_1, B_2, B_4	Single	215												
			Double	—												
18B	$DR_1 \times$ self when R_1 is red	Plant B_2	Single	200	3·0 : 1	172	28	101	39	60	87	32	53	14	7	7
			Double	66		50	16	35	14	17	25	11	14	10	3	3
19	,, when R_1 is flesh	,, C_1	Single	52	3·4 : 1	39†	13	14	24	12	11	19	7	3	5	5
			Double	15		12	3	4	9	2	4	6	2	—	3	—
18A	$DR_1 \times R_1$ when R_1 is red	Plants B_2, B_4	Single	97	1·2 : 1	49	48	51	46	—	25	24	—	26	22	—
			Double	77		35	42	49	28	—	21	14	—	28	14	—
31	$DR_1 \times DR_2$ when R_1 and R_2 are red and flesh respectively	Plant $B_2 \times C_1$	Single	84	3·5 : 1	66	18	40	21	23	34	14	18	6	7	5
			Double	24		20	4	12	3	9	10	3	7	2	—	2
1 (1)	$DR_1 \times R_2$ when R_1 and R_2 are red and flesh respectively	,, B_2	Single	115												
			Double	—												
1 (2)	,, when R_1 and R_2 are red and purple respectively	Plants B_2, B_4	Single	30	1·5 : 1											
			Double	19												
1 (3)	,, when R_1 and R_2 are red and claret respectively	Plant B_2	Single	6												
			Double	—												

* Plants related as sisters are indicated by the same letter of the alphabet.

† In two of these 39 the colour was not recorded.

In each of the several operations mentioned above, two sets of DR_1 cross-breds were used; in the one the recessive component (R_1) was sap-coloured (red or flesh), in the other cream. In the case of each of these recessive strains only a single individual plant was used to produce the DR_1 cross-breds from which F_2 was derived. In the various unions made with cross-breds containing cream (those above the horizontal line in the table), eight such cross-breds were used (A_1 to A_8), and in no case were doubles obtained in F_2. This absence of doubles, more especially in cases when the cross-bred was self-fertilised, or mated with DR_2 individuals afterwards shown to be themselves capable of producing doubles, points to the conclusion that the cream parent of the F_1 cross-breds was not carrying doubleness as a normal recessive character. A like result followed the use of cream in Experiment 1 (6) where the plant used as R_2 was not the individual used in the preceding experiments as R_1. Here the plant B_2, a DR cross-bred from a red recessive, carrying doubleness as a hidden character, as shown by the results of self-fertilisation (see Experiment 18B), produced exclusively singles when bred with a cream recessive (R_2). It happened that a white recessive was only used in two unions, and in both as R_2 (Experiments 1 (4) (5)). In one of these matings (Experiment 1 (5)) the DR_1 cross-bred with which the white was bred was probably carrying the double character; in the others (Experiment 1 (4)), where the cross-breds were derived from a cream, we have already seen that this was probably not the case. In neither of these unions did doubles occur in F_2.

In the remaining unions, where R_1 was sap-coloured (red or flesh), only three DR cross-breds were used; the results show that certainly two, and probably all three, were carrying doubleness as a latent character. Two only (B_2, C_1), as it happened, were self-fertilised, and both yielded a mixture of singles and doubles, as also was the case when they were bred together. The third plant (B_4) was, however, used in two other operations, being mated again with R_1, and also with R_2; in each case doubles occurred, so that there is little doubt that in this character the third individual resembled the other two. In other cases, a cross back with a sap-coloured recessive led to a suppression of doubles, as *e.g.*, in Experiment 1 (1), and thus, in all probability, the sap-coloured plant used as R_2 was not carrying doubleness.

In those unions where doubling occurred, the numbers indicate that this variation, which, from the nature of the case, cannot be exhibited either by the F_1 parents, or by the pure grand-parents, may appear in the F_2 generation in the proportions which we should expect in the case of a recessive character;* *e.g.*, in the three cases where the expectation in regard to surface character is 3 hoary : 1 glabrous (Experiments 18B, 19, 31C); the ratio of normal to double flowers is 3·0 : 1, 3·4 : 1, and 3·5 : 1 respectively, the agreement being closest in the case where the totals are largest. Moreover, the doubles are fairly evenly distributed among the different kinds of offspring, so that, whether the grouping is according to surface character, or to flower colour, this ratio is generally indicated. In the one case, where the expectation is equality, the ratio is 1·2 : 1. Grouping the plants into the smaller categories, according to surface character and flower colour, it becomes clear that the expected equality in the case of the purples is almost precise, whereas, among the reds, both hoary and glabrous, the discrepancy is much greater, the ratio being about 1·5 to 1.

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* Observations on some varieties of *Primula sinensis* seen at Messrs. Sutton's point to the same conclusion.

In the one combination where doubles resulted from the union $DR_1 \times R_2$ (Experiment 1 (2)), the ratio indicated was also 1·5 : 1. The question whether there is here a real deficiency of doubles, due to whatever cause, can scarcely be decided without further evidence.

The foregoing facts strongly suggest that, among the recessive strains, certain individuals only produce doubles, whereas others give rise exclusively to singles. The evidence, so far as it goes, further indicates that individuals carrying the double character occur frequently among the sap-coloured strains, but there is a slight presumption that the race of creams employed was not producing double-flowered offspring. White will be discussed later. These suggestions receive considerable support from the results obtained with the R_1R_2 cross-breds. In these cases, however, the problem becomes more complex, and the results less easy of analysis. Here the particular constitution of *both* the parents must be taken into account. Conceivably one or both, or neither, may be producing doubles. Unfortunately, offspring by self-fertilisation were not raised separately from the various recessive individuals, and hence direct proof as to their behaviour in regard to doubling is not available. A further complication may be found to affect the result; it may be that interference owing to reversion may occur in regard to doubling, as we have already seen to be the case in surface character and flower colour.

Of the various unions in the form $R_1 \times R_2$ recorded in Table I, only three yielded doubles in F_1, viz., copper × cream (Experiment 10), very light purple × cream (Experiment 11C), and red × dark purple (Experiment 15). In Experiments 10 and 11C, the cream form employed was the strain known as Princess May, a form which, like the sap-coloured types, produces both singles and doubles true to colour.* The cream plants used in the other unions in Table I belonged, with one exception, to another race, and yielded no doubles in F_1. Most of

* Some whites breed true to colour in the singles, but throw cream-coloured doubles. Till lately such whites were the sole source of cream doubles.

the individuals of this other race were certainly single, but no complete record of this character was made in this case, since no importance was attached to the point at the time. But though it cannot be affirmed with absolute certainty that no doubles occurred, it is most probable that such was the fact. Further investigation of the glabrous strains is now in progress, with a view to ascertaining how large a proportion of the individuals in any strain produce doubles, and whether the proportion of singles and doubles in each case is at all constant. Until such individual breeding has been carried out in the pure strains, and further crossing has given larger totals in the unions where doubles occur, these cases cannot be further analysed.

Families derived from reciprocals have, so far, given uniform results.

[Note, added December, 1904.

The posterity of the R_1R_2 cross-breds gave the following results. (See p. 37.)

Consideration of the results in the F_2 generation reveals several points of interest.

(1) In each case where R_1 and R_2 were both sap-coloured, the operation $R_1R_2 \times$ self gave doubles in F_2, the proportion being highest in the case of the one mating* which had also produced them in F_1. It seems by no means improbable that when doubling occurs in F_1 as well as F_2, both recessive parents will be found to be carrying the latent character, but that when the doubles occur only in F_2 one parent alone will produce doubles on self-fertilisation.

(2) In several experiments where a cream not belonging to the Princess May race had been used, no doubles resulted in F_2, when the F_1 cross-breds were self-fertilised. In the two matings in which this was not the case, the doubles were found only among the white and sap-coloured plants; the creams and the bicolors were all single, thus indicating a certain antagonistic relation in these cases between plastid colour and doubling. These results confirm the suggestion already put forward that the creams not belonging to the Princess May race were producing only singles. We can hardly attribute to mere coincidence—to the accidental choice, for various unions in various years, of certain individuals, which happened not to be producing doubles, though others of the race were—facts such as the following: (1) that no doubles were obtained either in F_2 from those bred with *incana*, or in F_1 from those bred with another recessive; (2) that in F_2 from (cream R × non-cream R) × self, doubles, when they occurred, were confined to the non-cream plants.

(3) In the one experiment of the form $R_1R_2 \times$ self in which a Princess May cream was used, the distribution was strikingly reversed.

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* See p. 35.

R_1R_2 × self (Experiments 18, 19).

Colour of R parents.	Individuals used in F_1.	Proportion of singles and doubles in F_2.									
		Total single.	Total double.	+ Sap − plastid.		+ Sap + plastid.		− Sap − plastid.		− Sap + plastid.	
				Single.	Double.	Single.	Double.	Single.	Double.	Single.	Double.
White$_6$ × cream$_5$	Plant A	75	—	—	—	—	—	—	—	—	—
White$_6$ × flesh	,, B	45	—	—	—	—	—	—	—	—	—
Dark purple × white	,, C	16	—	—	—	—	—	—	—	—	—
	,, C′	33	14	31	10	—	—	2	4	—	—
White$_6$ × red	,, D	8	1	7	1(H)	—	—	1	—	—	—
	,, D′	37	10	29	10(H)	—	—	8	—	—	—
White$_8$ × copper	,, E	48	19	36	13	—	—	12	6	—	—
Cream$_5$ × white$_1$	,, F	110	—	—	—	—	—	—	—	—	—
Dark purple × cream$_5$	,, G	88	—	—	—	—	—	—	—	—	—
Cream$_1$ × flesh	,, H	25	—	—	—	—	—	—	—	—	—
Cream$_3$ × red	,, I	130	58	82	47	24	—	20	11	4	—
Cream$_6$ × light purple	,, K	73	42	41	37	10	—	17	5	5	—
Flesh × cream (Princess May)	,, L	44	16	33	—	1	12	10	1	—	3
Copper × flesh	,, M	20	2	—	—	—	—	—	—	—	—
Flesh × dark purple	,, N	28	8	—	—	—	—	—	—	—	—
Red × dark purple	,, O	16	9	—	—	—	—	—	—	—	—
Dark purple × light purple	,, P	20	3	—	—	—	—	—	—	—	—

(H) = hoary.

$R_1R_2 \times R_1$, $R_1R_2 \times R_2$, $R_1R_2 \times R_3$, and $R_1R_2 \times R_2R_3$ (Experiments 20—27).

Form of union.	Individuals used in F_1.	Total single.	Total double.
(White × red) × red	D′	21	14
,, × copper	D′	13	10
,, × white	D′	22	—
,, × cream	D″	12	—
(White × flesh) × flesh	B	16	—
	B′	39	—
,, × red	B′	32	—
,, × white	B′	18	—
,, × cream	B	21	—
(Cream × red) × red	I′	9	18
,, × cream	I′	16	—
(Cream × flesh) × flesh	H′	19	—
,, × copper	H′	16	—
,, × white	H	24	—
,, × cream	H	17	—
(Dark purple × cream) × dark purple	G′	24	—
,, × cream	G′	23	—
(White × red) × (red × dark purple)	D × O′	38	5

Doubles occurred in F_2, but with one exception they were confined to the plants with coloured plastids (cream and bicolor), none appeared among the sap-coloured selfs, the one exception being a white. As previously mentioned, white commonly occurs in F_2 from a cross between cream and sap-coloured recessives, for the plastid- and sap-characters are recombined in the gametogenesis of F_1.

(4) With regard to the interpretation of the results obtained with the white race there is more uncertainty, as we have as yet no evidence from the *incana* cross-breds. Doubles were absent in F_2 raised from four self-fertilised cross-breds (A, B, C, and F), to produce which certainly two and probably three white individuals were used. Two of the cross-breds were obtained from matings between white and cream, two from white × sap-colours. In these cases the character of the whites has to be inferred from the behaviour of only four of their gametes. Again, we have seen that an *incana* cross-bred (Table II, plant B_4) which yielded doubles on two occasions when crossed with sap-colours, produced none when crossed with a white: here a numerous F_2 offspring represent as many gametes of the recessive white. On the other hand, four other R_1R_2 cross-breds (C′, D, D′, E), derived from unions between white and sap-colours produced doubles, C′ being own sister to C which gave none. In the case of C′ and E the doubles were distributed alike among hoary and glabrous, coloured and white plants, whereas in the case of the two sister cross-breds, D and D′, the doubles

only appeared among the hoary, and therefore coloured plants. The evidence points here as in some previous cases to an association or coupling of doubling with another character. If experiments on a larger scale should confirm these results, then any hypothesis concerning the production of doubles on crossing recessives must take into account the following possibilities: (1) absence of doubles; (2) occurrence of doubles in all categories; (3) occurrence of doubles in certain categories only. The fact that of sister cross-breds one may give rise to doubles, and another not, indicates differentiation (as regards doubling) among the germ cells of one individual, since here interference owing to reversion can scarcely be in question. Whether the three kinds of results observed in F_2 can be satisfactorily accounted for on the supposition that of the recessive parents, one, or both, or neither may be producing doubles, and that when a mixture of singles and doubles occurs, there is a corresponding differentiation among the germ cells of the individual producing them, is not altogether clear. We can, therefore, form no final conclusion as to the behaviour of the white race in regard to doubling, since it remains uncertain whether, when doubles occurred, they are to be regarded as derived from both parents, or only from the non-white, though at present the evidence favours the latter view.

(5) The F_2 generation obtained from a cross back with one of the parent strains showed an absence of doubles when the recessive bred with F_1 was the non-sap-coloured form. When the sap-coloured type was introduced twice the results varied, some cross-breds gave doubles, others not. If the suppositions mentioned in (4) are correct, this is to be expected.]

V. *Experiments with* M. sinuata.

'Curtis's Botanical Magazine' for 1900 contains a coloured figure of a white-flowered glabrous variety of *M. sinuata*, together with the following statement:—"*M. sinuata v. oyensis* is a native of the Ile d'Yeu off the coast of La Vendée, where it grows associated with the typical form." It is described as "an annual or biennial branching green herb, 1 to 2 feet high, somewhat sparsely furnished with stalked glands on the stems, leaves, calyces, and pods, but quite destitute of the dense felt-like greyish tomentum characteristic of typical *M. sinuata.*" Specimens of this variety, raised in the Botanic Garden, were kindly placed at our disposal by Mr. Lynch. Reciprocal crosses were made between the variety and the type form which occurs wild on the south and west coasts of England. Unfortunately the attempt to rear vigorous healthy plants of the type form was unsuccessful. Some few plants produced flowers which furnished a supply of pollen, but they invariably perished before setting fruit; the cross-breds obtained were, therefore, all from the mating var. ♀ × type ♂. These cross-breds—one family of twelve plants—were covered with a tomentum, and were indistinguishable from the type form. Here, as in the similar experiments with *incana*, the hoary character is dominant.

Matings between the glabrous variety of *sinuata* and *incana* showed considerable sterility. A few good seeds were obtained, from which three cross-breds were raised. These plants have not yet flowered. In regard to leaf outline and character of the tomentum, they showed a condition intermediate between the type forms of the parent species. The stalked glands, characteristic of *sinuata*, were absent; evidently gland-formation behaves as a recessive character on crossing with the non-glandular *incana*.

VI. *Summary of Conclusions from Experiments with Matthiola.*

1. Various matings of Stocks yield heterozygotes which are reversionary, and the occurrence of such reversion may interfere with the appearance of a recessive character.

2. Such interference with regard to the recessive character glabrousness occurs in all unions of the form $R_1 \times R_2$, $DR_1 \times R_2$, and $DR_1 \times DR_2$* when either or both of the recessives is a type with uncoloured sap (*i.e.*, a white or cream); in such cases all the resulting cross-breds are hoary.

3. Curious specific results affecting physiologically distinct characters follow the use of specific types, which, so far, seem to differ in flower colour alone. Whether the presence of these dissimilar colours in reality causes the difference in results is still unknown, and it is not impossible that the essential distinction may be some quality with which the flower colour happens to be associated.

4. The union of certain allelomorphic characters, when these are carried by the gametes of pure-bred types, may give rise to reversionary forms, whereas when the same combination of characters is made by the union of the gametes of cross-breds, such reversion does not always occur. In certain cases it may be altogether wanting, or it may occur in one character and not in another, or in other cases, again, the two kinds of unions may produce similar results. Illustrations of such cases may be briefly stated thus: (1) Pure-bred glabrous white × pure-bred glabrous red produces *hoary purple*, but a cross-bred gamete carrying white colour and glabrousness meeting either a pure-bred, or a cross-bred sister gamete carrying red colour and glabrousness gave *glabrous purple*. *In the former case there is reversion both in surface character and colour; in the latter the two characters are dissociated, and reversion occurs in the one* (*colour*) *and not in the other* (*surface*

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* D and R are used throughout to denote the dominant character hoariness and the recessive character glabrousness.

character) (see Experiments 4, 28A, 28B). (2) Pure-bred glabrous white × pure-bred glabrous cream also produces *hoary purple*, but a cross-bred gamete carrying whiteness in conjunction with glabrousness, on meeting either a pure-bred, or a cross-bred sister gamete carrying cream colour and glabrousness yielded *glabrous white. Here, also, there is in the former case reversion in both characters; in the latter it occurs in neither. Instead, white is now dominant over cream, and the glabrous character is inherited* (see Experiments 3, 30A, 30B). (3) When certain DR cross-breds containing different recessives as, *e.g.*, cream and red, are mated together (gametes carrying these two colours + glabrousness presumably meeting each other), *the result of such union is certainly as regards surface character and possibly also as regards colour, the same as when similarly coloured pure-bred recessive types are bred together* (see Experiments 8 and 31A, where cream glabrous × red glabrous appears to give red hoary in both cases).

5. Cross-breds containing the same dominant (white *incana*), but a different recessive, produce, at least, one set of gametes which are carrying a similar combination of recessive characters (whiteness and glabrousness). When such cross-breds were bred together, and when, therefore, these particular recessive gametes must have met, such unions produced either (1) individuals exhibiting this same combination of recessive characters (viz., whiteness and glabrousness), or (2) individuals which, whatever may prove to be their colour,* reverted to the dominant (hoary) type in surface character. In (1) both cross-breds contained a sap-coloured recessive, and in (2) one contained a sap-coloured and the other a cream-coloured recessive, see Experiments 21A, 21B, where

(Red glabrous × white hoary) × (Cream glabrous × white hoary) and
(Cream glabrous × white hoary) × (Flesh glabrous × white hoary)

gave no white recessives: whereas in 21C

(Red glabrous × white hoary) × (Flesh glabrous × white hoary)

yielded the expected proportion. It happened that no matings were made with cross-breds containing a white recessive. Had such cross-breds been used, it is probable that the result in this respect would have been similar to those obtained with cream, and that here as elsewhere the general rule holds that the one result follows when two sap-coloured recessives are employed, and the other when sap colour is absent in one or both of the recessives.

6. When extracted recessives are mated with pure-bred recessives, the result is dependent not merely upon the visible characters of the

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* Whether these individuals were among the white-flowered dominants cannot be certainly determined until the results in F_3 have shown which of the colours obtained in F_2 were produced by these particular gametes.

"extracted" plant and of the pure-bred race, but also upon the composition of the cross-bred from which the recessive in question is extracted: *e.g.*, a glabrous white extracted from a DR cross-bred containing a cream recessive, when mated with a pure-bred cream recessive, gave a glabrous offspring; but a glabrous white extracted from a cross-bred which did not contain cream, when similarly mated, yielded hoary plants. These diverse results were obtained from what appear to be precisely similar pairs of whites and creams; nevertheless, the result varied according as the new recessive was or was not similar to the one introduced in the original cross. A parallel result occurs when an "extracted" glabrous white derived from a DR cross-bred, where R is cream, was bred with a pure-bred glabrous white; the plants obtained were all hoary. Here, again, reversion occurred when the newly-introduced recessive differed in colour from the original R.* (A separate experiment in which this relation appeared not to hold was open to suspicion of error on other grounds.) We thus arrive at the result that two apparently similar recessive parents may produce offspring unlike themselves.

For comparison the following table exhibits the results which we know to occur when certain *pure-bred* types are intercrossed, and those which apparently take place when one or both of the meeting gametes is derived from a *cross-bred*.

Combinations of allelomorphs borne by the uniting gametes.	Results known to occur when both gametes are from pure-breds.	Results indicated.	
		1. When one gamete is from a pure-bred and one from a cross-bred.	2. When both gametes are from cross-breds.
White glabrous and cream glabrous.	Purple hoary (Experiment 3).	White glabrous (Experiment 30A) (colour unknown), hoary (Experiment 80, Report I).	White glabrous (Experiment 30B), purple hoary (Experiment 31A).
White glabrous and red glabrous.	Purple hoary (Experiment 4).	Purple glabrous (Experiment 28A).	Purple glabrous (Experiments 28B, 31C).
White glabrous and white glabrous.	White glabrous.	(Colour unknown) hoary (Experiment 17A).	White glabrous (Experiment 31C), white hoary (Experiment 31A).
White hoary and white glabrous.	Purple hoary (Experiment 19, Report I).	—	White hoary (Experiments 30B, 31A, 31B, 31C).
Cream hoary and cream glabrous.	—	Non-cream hoary (Experiment 30A).	Cream hoary (unnumbered experiment).

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* Parallel experiments with sap-coloured recessives have not yet been made.

The conclusion that the meeting of the gametes in the several experiments, was that given in this table, is arrived at by a tentative analysis of each case. The experimental analysis has not yet proceeded far enough to enable us to state the precise cause of the dissimilarity of results in certain cases. There is, however, little doubt that further experiments will bring the whole into one uniform system, as has already been done for other results in F_2, some of which, at first sight, seemed similarly aberrant.

7. Doubling frequently behaves as a Mendelian recessive, and may show definite association with physiologically distinct characters. The evidence strongly suggests that certain Ten-week recessive types produce exclusively singles (some cream and perhaps some white races), and that others (notably the sap-coloured forms and the cream strain, Princess May), constantly yield singles and doubles mixed. Among these latter there is probably differentiation in regard to doubling, not only among the several individuals of any race, but also among the several gametes of one individual.

8. The differentiation previously established for the female gametes of cross-breds is equally true of the male.

9. The hoary character appears in F_1 when the type form of *sinuata* and the white-flowered glabrous variety *oyensis* are bred together. The relation of hoariness to glabrousness is here as in *incana*, that of dominant to recessive.

The stalked glands characteristic of *sinuata* (both type and variety), disappeared when *incana* and *oyensis* were crossed together. Gland formation evidently behaves as a recessive character when *sinuata* is crossed with the non-glandular *incana*.

10. We have now an explanation of many of the experiments which in the earlier Report were classed as aberrant (see Report I, Tables XIV and XV), and now appear to be due to unexpected reversion in the heterozygote. We thus account for the two experiments (79 and 80 in Table XIV), previously regarded as aberrant, in which dominant offspring were produced when the expectation was all R. On the supposition (already discussed in Report I, p. 81), that the group of 9 experiments in the same Table, where some recessives occurred when the expectation was all D, are probably to be explained as cases of the "false hybridism" of Millardet, we have left only a single result (Experiment 10), in Table XIV, which appears to be at variance with the Mendelian account. In this case the aberrant result occurred when a half-hoary strain was used as the dominant type, and no further experiments with this strain having yet been made, this one result still remains unexplained. Of the aberrant cases where the expectation was a mixed offspring (Table XV), many can now be similarly brought into line. Nine of these cases occurred in experiments where the expected result was 1 D : 1 R; of these only two

remain unaccounted for. In one of these (Experiment 73B), the exceptional result was obtained from only one individual, while 7 others gave a Mendelian result (Experiment 73A); it seems, therefore, not impossible that this exceptional result may have been due to the selection of a seed-parent in the final cross, which was not really a DR but a DD produced by accidental self-fertilisation. With regard to the other (Experiment 60), we have as yet nothing further to state, this being another experiment in which the half-hoary strain was employed. For the same reason further comment is deferred respecting most of the cases which occurred where the expectation was 3 D : 1 R, and in which either a half-hoary, or a fully hoary annual type was employed. The other cases in this group are possibly due either to the same cause as that suggested in the case of Experiment 73B (Experiment 100A); or, where the deviation from expectation consists in a deficiency and not a complete absence of recessives, to some disturbance affecting the usual symmetrical distribution of the gametes (Experiments 95, 96, 107A).

SALVIA HORMINUM.

This species was chosen for experiment as offering a good case of a character with three well-marked contrary or alternative forms. The wild plant is found in the Mediterranean region, and is remarkable for the coloured bracts which terminate the stem axes. It is described as occurring wild under two forms,* in the one the flowers and terminal bracts are coloured violet, in the other pink; a third (albino) form with bracts and flowers white is in cultivation. All three strains breed true.

Of previous records of cross-breeding experiments with this species we have those of H. Hoffmann.† From crosses between the two coloured forms he obtained the following results:—(1) a mixed offspring in F_1, the individuals being similar in colour to one or other parent, none being intermediate in tint; (2) a second generation (F_2), also frequently mixed, whether derived from violet or from pink seed-parents.

Details of the experiments are not given; we are not told whether emasculation was performed in the first cross or not, nor whether any other precaution against chance cross-fertilisation was taken beyond placing the plants in a room. It is, however, stated that in the later generations the possibility of such cross-fertilisation was not definitely excluded. In the light of the results about to be described it seems clear that little value can be attached to Hoffmann's numbers. The mixed result obtained by him in F_1 may probably be explained by the supposition that the violet plants were not pure but cross-breds, while the fact that in F_2 both pink and violet plants were obtained from pink seed-parents, must undoubtedly be attributed to crossing.

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* Engler u. Prantl, 'Die Natür. Pflanz.,' vol. 4, 3*a*, p. 274.

† 'B. Z.,' 1887, Band 45, p. 755.

In the present experiments the method of procedure was as follows:—the plants for convenience of handling were grown singly in pots and covered with muslin. In the earlier experiments some unemasculated flowers were allowed to open under cover with those prepared for crossing, but in the crosses made in the second year this possible source of error was avoided. The manipulation of the flowers was somewhat troublesome; both emasculation and pollination were carried out under a lens. Emasculation was performed before the corolla exceeded the calyx tube in length. Careful handling is necessary as the buds break somewhat readily from their pedicels. By holding steady the free end of the bud, the calyx tube can safely be slit backwards, and a window made in the side of the hood of the corolla; through this opening the stamens are at this stage easily withdrawn bodily by gently gripping the filaments at the point of curvature. Pollination was effected by inserting the stigmas into the slit of a ripe detached anther, but although a number of pollen grains were often observed to be adhering to the stigmatic branches, the full complement of seeds (four), was not very often obtained from artificially fertilised flowers.

Some 20 plants of the three forms were raised from seed; of these all came true to the specified colour except two, which should have been pink but were violet. The suspicion that these two individuals would prove to be cross-breds was fully confirmed later, for both gave rise to a mixed offspring of violet and pink; the remaining plants bred true to colour on self-fertilisation.

In the following account the expressions V_1, V_2, P_1, P_2, W_1, W_2, etc., will conveniently distinguish the different individuals according to their colour.

(*a*) From the accompanying Table (see p. 46) it is seen that in each of the four unions W × V, V × W, P × V, and V × P the result is the same: the offspring are all violet; pink and white are thus both recessive to violet. Moreover, the violet colour of the cross-breds is indistinguishable from that of the pure form.

(*b*) In the unions between the pink and white strains, however, the results appear less concordant; the majority of the offspring are again violet, but in one mating (Experiment 5) the offspring were mixed, and included three whites, and in another (Experiment 6B) the five offspring obtained were all pink. In view of the fact that from every union except No. 5 a uniform result was obtained, it is scarcely possible to doubt that the mixture in this case is attributable to accident, and that the three whites were either accidental selfs or strays. With regard to Experiment 6B, the supposition at the time was that here, also, some

Table I.—Offspring obtained from Reciprocal Crosses between the Three Different Forms.

Date.	Number of experiment.	Parentage.	Offspring.		
			V.	P.	W.
1901	1	$W_1 \times K$	2		
		$W_1 \times V_4$	14		
		$W_2 \times V_4$	3		
		$W_3 \times V_4$	6		
		$W_4 \times V_6$	1		
	2	$V_7 \times W_1$	3		
		$V_7 \times W_4$	2		
	3	$P_1 \times V_4$	3		
		$P_1 \times V_7$	3		
		$P_4 \times V_7$	1		
	4	$V_1 \times P_2$	10		
	5	$W_1 \times P_1$	13		3
	6A	$P_1 \times W_1$	6		
		$P_1 \times W_3$	10		
	6B	$P_4 \times W_2$		5	
1902	7	$(W_4 \times \text{self}) \times (P_4 \times \text{self})$	2		
	8	$(P_1 \times \text{self}) \times (W_3 \times \text{self})$	18		
		$(P_1 \times \text{self}) \times (W_4 \times \text{self})$	7		

unknown error had occurred either in marking the particular flowers crossed, or in gathering the seed, and that the five pink plants must have resulted from self-fertilisation. If this view were correct, and if, therefore, from the results of Experiments 5 and 6A we might conclude that a cross between pink and white would always produce violet, it followed that *any* white or pink plant could be regarded as pure, that a pink could not be obtained from a white, nor a white from a pink (except as a variation *de novo*), and that unions in which any one of these five pink plants was employed should give the same results as similar unions in which other pink individuals were used. If, on the other hand, the five pinks did actually result from the union $P_4 \times W_2$, it is clear that *pink* plants might be cross-breds, that a pink could be obtained from a white, and probably, therefore, conversely a white from a pink; that unions with one of these five cross-breds would give results different from those obtained when a pure-bred pink was employed; and, further, that the result of a first cross between a white and a pink will vary with the individuals employed. In order to settle the point in question some of the five pink plants were used in several later unions instead of pink individuals *known* to have resulted from the self-fertilisation of pink parents. The difference of result in the two cases (compare Experiments 7 and 8 with Experiments 24A, 24B, 25A, 25B) fully disposes of any suspicion of experimental error in the earlier cross, and proves beyond doubt that the five pinks of Experiment 6B were genuine cross-breds. For when whites and pinks known to be pure-bred were crossed together (Experiments 7 and 8), the offspring, twenty-seven in number, were all violet, a result entirely in agreement with that obtained in Experiment 6A, and, we may suppose, in Experiment 5 also. But when similar pure-bred whites were crossed with the supposed pure pinks of Experiment 6B, the offspring, which were mixed, always included some whites, thus again indicating that the pink parent was not pure, but PW in composition. If yet further evidence were needed to substantiate this view, it is afforded by the experiments recorded in Table II, which were designed to test the point as to whether white plants could be obtained from pink, or *vice versâ*. For this purpose a large number of seeds were collected from various pure-bred white and pink plants, and from three of the five pinks of Experiment 6B, all having been grown under conditions which exposed them to the possibility of being crossed both with the pure types and with cross-breds. In order to avoid any chance of error through the germination of stray seeds the experiment was duplicated; some plants were raised in the Botanic Garden allotment, and others away from Cambridge. In the new localities seeds from white plants only, or from pink plants only, were sown in

Table II.—Offspring obtained from Chance Fertilisation of (*a*) Pure-bred Whites, (*b*) Pure-bred Pinks, (*c*) Pink Cross-breds, which were left Uncovered.

	Number of experiment.	Parentage.	Number of seed parents.	Offspring.		
				V.	P.	W.
(*a*)...	9	$(W_1 \times \text{self}) \times ?$	2	106	—	147
		$(W_2 \times \text{self}) \times ?$	1	77	3	54
		$(W_3 \times \text{self}) \times ?$	1	30	—	34
		$(W_4 \times \text{self}) \times ?$	2	152	—	175
		$(W_1 \times \text{self}) \times ?$ $(W_2 \times \text{self}) \times ?$ $(W_3 \times \text{self}) \times ?$ $(W_4 \times \text{self}) \times ?$	?	220	2	293
(*b*)...	10	$(P_1 \times \text{self}) \times ?$	3	56	81	—
		$(P_4 \times \text{self}) \times ?$	2	28	50	—
(*c*)...	11	$(P_4 \times W_2) \times ?$	3	50	186	29

each garden.* In every case the results showed that the exposed plants must have been cross-fertilised to some extent, for all the different sets of offspring were mixed. In the case of the pure-bred pinks (Experiment 10), they were violet and pink (131 P, 84 V), but in accordance with expectation none were white. In the case of the three pinks of Experiment 6B, the offspring were also mixed (Experiment 11), but here all three colours appeared (186 P, 50 V, 29 W), and we thus have further proof that the five plants of Experiment 6B were genuine cross-breds, that in certain cases P × W shows dominance of P, and that such pink cross-breds will again yield whites (presumably both on self-fertilisation and on fertilisation with whites).

Since it is evident that some white and pink plants, when crossed together, yield only violet offspring, while others, when thus crossed, produce pinks, it becomes important to know whether we can recognise these different kinds of individuals, and so predict their behaviour in any given union. It will be noticed that neither of the two parents of the five pink cross-breds (P_4 and W_2) happened to have been used in the other matings of pinks and whites (see Table I). The only further piece of information which the Table affords is the fact that, although P_4, when crossed with white, gave pink, *the offspring of* P_4, by self-fertilisation, when thus crossed, produced violet plants. In this connection, the results obtained in Experiment 9 are of considerable interest. In this experiment, offspring by self-fertilisation of the various white plants used in the crosses with pinks and violets were not covered, and fertilisation was left to chance. Crossing evidently occurred, for, in every case, the next generation was mixed; the total number of plants obtained were 585 V, 703 W, and 5 P. Now it is conceivable that these five pinks were all descended from W_2; three certainly were, and the remaining two came from a mixed lot of seeds, some of which were gathered from W_2—the individual which crossed with P_4 yielded pink offspring. Even if this were so, however, it is surprising that, with random fertilisation, the number of pinks should be so small as compared with the violets obtained from the same plant. An error, due to germination of stray seeds, is here out of the question, for the five pinks occurred among the plants raised away from Cambridge; the only possible source of error would be in harvesting, but, as this is not very probable, the result must be considered as it stands. Putting all the facts together, we have

$$\begin{array}{ccc} (1) & (2) & (3) \\ P_4 \times W_2. & (P_4 \times \text{self}) \times \text{white.} & (W_2 \times \text{self}) \times \text{pink (presumably).} \\ | & | & | \\ \text{P} & \text{V} & \text{P} \\ & & \text{some with V and W} \end{array}$$

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* We are greatly indebted to the kindness of Miss Elliot, of Newnham College, and of Mrs. Caulfield Reid, formerly of Newnham College, for the raising and recording of some hundreds of these plants.

Of the ancestry of the individuals, P_4, W_2, we know nothing, they may have been derived from pure parents, or "extracted" from cross-breds. Now we already know cases in Stocks and Sweet Peas among plants, and in mice among animals, where "extracted" individuals behave differently from the pure-breds which they resemble. In the case of Stocks, we know that pure-bred glabrous white × pure-bred glabrous cream yields purple hoary, but "extracted" glabrous white × pure-bred glabrous cream may give glabrous plants with colourless sap. Again, in the white-flowered Sweet Pea, known as Emily Henderson, there are two forms, with round and long pollen respectively. A cross between the two produces Purple Invincible with long pollen, which, when self-fertilised, yields again, besides a variety of other types, white-flowered plants, with long pollen, and others with round pollen. As far as our experience has gone, such extracted "long" and "round" whites give whites (long) and no reversion to purple.* The suggestion here made is that the Salvia result may possibly be analogous with that in the Stock and the Sweet Pea; that, in Experiments 5 and 6A, the cross was between individuals, either or both of which were pure-bred, but that in Experiment 6B, it happened to be between individuals, both of which were "extracted." If such were the case, the occurrence of reversion to violet in the former cross, and of dominance of pink in the latter, would only be in accordance with what we already know in other instances. Until we have before us the evidence from unions between individuals known to be "extracted" —experiments which are in progress—no more definite statement can be made.

Unfortunately, nothing can be ascertained regarding the composition of the five pinks of Experiment 9, since all plants obtained in this experiment were destroyed as soon as recorded. Nor can the supposition that the seed-parent of these plants (W_2 × self) may have been crossed with an "extracted" pink—the only explanation which suggests itself—be immediately tested, since, as yet, we know nothing of the results of such unions. We cannot foretell whether the offspring of "extracted" parents will behave like such parents or like pure-breds, in the cases where the two differ, nor whether such offspring will yield a mixture of the two kinds of individuals, though the evidence of Experiment 9, so far as it goes, is against the second alternative.

All the six kinds of violet-coloured cross-breds in accordance with expectation yielded a mixed offspring when self-fertilised or fertilised *inter se.* When the original union had been between violet and pink or between violet and white, the colours exhibited by the F_2 generation were those of the original parents, violet and pink only in the former

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* For a fuller account of these results, see pp. 82 and 96.

Table III.—Offspring obtained from Violet Cross-breds by Self-fertilisation or Fertilisation *inter se.*

Number of experiment.	Parentage.	Number of seed-parents.	Offspring.		
			V.	P.	W.
12	(W × V) × self or *inter se*	1	24	—	7
13	(V × W) × ,,	4	26	—	17
14	(P × V) × ,,	1	45	20	—
15	(V × P) × ,,	7	775	245	—
16	(W × P) × ,,	2	59	25	34
17	(P × W) × ,,	12	255	92	114

case, violet and white only in the latter. In Experiment 15 when a large sowing had been made and more than 1,000 plants flowered, the numbers obtained are in good agreement with expectation, the ratio of violet to pink being as 3·1 : 1 instead of 3 : 1. In the reciprocal cross (Experiment 14) very much smaller numbers were recorded, and the result showed a slight excess of recessives. In the two experiments where the cross was between violet and white, the numbers were smaller still; in the one case (Experiment 12) the result was almost exact (24 V : 7 W), but in the reciprocal (Experiment 13) the number of recessives was much too high (26 V : 17 W).

The two remaining experiments (Experiments 16, 17) are cases in which we should *a priori* expect that all three colours would appear in the F_2 generation in the ratio 1 P : 2 V : 1 W, and further that such pinks and whites would henceforth breed true, but that the violet plants would prove to be cross-breds and yield a mixed offspring in the next generation. We should, in fact, be dealing with a case of simple reversion unaccompanied by the complication of disintegration or resolution of the allelomorphs, a case, therefore, in which we can distinguish among the F_2 individuals the cross-breds from the two parental forms. The facts observed will be seen to agree well with expectation. Self-fertilisation of the violet-coloured PW cross-breds yielded all three forms, the ratios obtained in the reciprocal crosses being respectively ·72 P : 2 V : ·89 W and ·84 P : 2 V : 1·1 W.

When violet-coloured cross-breds of whatever composition are crossed back with an original parental form, such parental form not being violet, the expectation is that the offspring will be mixed, of two colours in equal numbers, half being violet and half the colour of the form introduced in both unions. In two or three cases the numbers obtained were very small, in Experiments 20 and 21 too small probably to be conclusive, the offspring which were all violet being only two in the one case and only six in the other. That a mixed offspring would

Table IV.—Offspring obtained from Violet Cross-breds, by crossing back with one of the original Parent Forms, such Parent Form not being Violet.

Number of experiment.	Parentage.	Number of seed parents.	Offspring.		
			V.	P.	W,
18	(W × V) × W	5	16	—	17
19	(V × W) × W	1	5	—	1
20	(P × V) × P	1	2	—	—
21	(V × P) × P	1	6	—	—
22	(P × W) × P	2	2	6	—
23	(P × W) × W	2	14	—	9

undoubtedly have been obtained if a larger number had been raised we may safely conclude from the fact that the same cross-breds when self-fertilised (Experiments 14 and 15) did yield both parental forms. In the other cases the offspring showed the two anticipated colours, and though generally in unequal proportions, the discrepancies are not greater than might be expected to occur with such small totals.

From the very definite and comparatively simple symmetrical grouping of the ovules and flowers in this species—four ovules to each flower and six flowers to each whorl (verticillaster) it was hoped that some indication of a definite symmetrical disposition of the different kinds of female gametes in the cross-bred might be obtained. With this end in view all the flowers of several consecutive whorls of a cross-bred were crossed back with the original recessive form, the order in which the flowers opened was noted,* and the seeds of each were harvested and sown separately. The experiment requires that every ovule should be fertilised, that every seed should germinate, and that every seedling should reach maturity. Unfortunately, however, the full number of seeds is not often produced in artificial fertilisation, and no sufficiently continuous record was obtained. Only in some half-dozen isolated instances was the experiment successful; the results from these particular flowers showed that in one case all four ovules were recessive, in another two were dominant and two recessive; in two cases three were dominant and one recessive, and in two cases one was dominant and three recessive. It is thus evident that if the individual cross-bred produces, as we have reason to believe, equal numbers of allelomorphic ovules, this equality is not necessarily bound up with a corresponding equality of distribution in each individual flower.

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* Of the two axillary cymes composing each whorl, the central flowers usually open simultaneously and before the younger lateral flowers; these latter, in fact, do not generally unfold until after the central flowers of some of the higher nodes are open.

Table V.—Offspring obtained from Reciprocal Unions between Pure-bred Whites and Pink Cross-breds.

Number of experiment.	Parentage.	Number of seed parents.	Offspring.		
			V.	P.	W.
24A	(W_1 × self) × P cross-bred	3	16	—	16
24B	(W_4 × self) × P cross-bred	2	12	—	7
25A	P cross-bred × (W_3 × self)	2	10	—	7
25B	P cross-bred × (W_4 × self)	1	4	—	2

In the case where P × W yields V we have seen that the result of the cross PW × W is a mixed offspring, half violet, half white (Experiment 23), but in a case where P × W yields P, what are we to expect from a union between such cross-breds and pure-bred whites? A mixed offspring, of which half will be white, arising from the meeting of the white-bearing gametes of the pure form with the similar gametes of the cross-bred, we may perhaps predict, but what will be the colour produced when these same gametes unite with the pink-bearing gametes of the cross-bred?

According to the results of Experiments 24A, 24B, 25A, 25B, such unions yield violet, for the mixed offspring obtained was composed of about the expected proportion of white and coloured individuals (half-and-half), the coloured plants being all violet. Until we know more of the behaviour of "extracted," as compared with pure-bred individuals, it is impossible to say whether the above result would always follow when such pink cross-breds are mated with a white form, or whether by union with an "extracted" albino a mixed offspring would not be obtained, consisting of equal numbers of pinks and whites, instead of violets and whites.

Table VI.—Results obtained when Offspring of a Cross between the Dominant (Violet) Type and one Recessive Form are Crossed with the other Recessive Form.

Number of experiment.	Parentage.	Number of of seed parents.	Offspring.		
			V.	P.	W.
26	(W × V) × P	1	3		
27	(V × W) × P	1	4		
28	(P × V) × W	2	10		
29	(V × P) × W	1	2		

In Table VI are given the results obtained from operations of the form $DR_1 \times R_2$. The total number of plants raised was 19, and all were violet, a result completely in harmony with expectation, since on the supposition that we are right in attributing the exceptional result in Experiment 6B to the use of an "extracted" in place of a pure-bred plant, we may conclude *that a cross in any form between two types of unlike colour will produce the same colour result, viz., violet.*

Summary of Conclusions from Experiments on Salvia Horminum.

1. The results obtained from reciprocal crosses between the different forms entirely support Mendel's conception of germ purity.

2. Of the three strains, violet, pink, and white, the two latter are both recessive to the first-mentioned form. Cross unions between violet and either of the other colours exhibit the simple Mendelian phenomenon of dominance in F_1 and segregation of the two parental forms in F_2, the proportions approaching the Mendelian ratios in cases where fairly large numbers are recorded.

3. Cross unions between the two recessive forms in one instance showed dominance of pink, and in the others reversion to violet. In explanation of these diverse results it is suggested that dominance of pink occurs when both the parents are "extracted," but that otherwise there is reversion to violet.

[Compare the results obtained with the Sweet Pea "Emily Henderson" and with Stocks.]

4. The violet cross-breds resulting from unions between pinks and whites yield all three forms in the next generation in the ratio 1 P : 2 V : 1 W; the F_2 cross-breds are thus distinguishable from both the extracted types. The pink cross-breds (formed presumably when an "extracted" pink is crossed with an "extracted" white) yield only the two parental forms—pink and white.

5. When a cross-bred produced by mating the dominant (violet) type with one of the recessive forms, is crossed with the other recessive form, *i.e.*, in operations of the form $DR_1 \times R_2$, the offspring, in accordance with expectation, are all violet.

RANUNCULUS ARVENSIS.

This species occurs under three forms. In the only British type the carpels are covered with numerous long spines; in the var. *tuberculatus* the spines are replaced by obtuse tubercles, while in the third form, var. *inermis*, the veins form anastomosing ridges which are unarmed. All three forms are described by Koch,* who mentions Bonn as a ocality where the unarmed variety is to be met with, adding, however, that it is very rare. Godron* states that he had been accustomed for several years to find *inermis* in a field at la Malgrange, near Nancy, but up to that time it had only been recorded from the environs of Bonn, and was extremely rare, whereas the armed variety *tuberculatus* was less uncommon. These forms had also been noticed in the corn-fields around Nancy by an earlier observer.†

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* 'Syn. Flor. ger. et helvet.,' éd. 1, 1837, p. 18.

R. arvensis was another of the many species used by Hoffmann‡ in his cross-breeding experiments, and here, as in *Salvia Horminum*, the want of uniformity in his results suggested the possibility of experimental error (as he himself realised), and the likelihood that a repetition of the experiments would yield a constant result. This has in fact proved to be the case.

The plants used in our experiments were a single stray individual of the type form found growing in the allotment, and some half-a-dozen specimens of each of the two varieties (*tuberculatus* and *inermis*) obtained through the kindness of Mr. Lynch from the Botanic Garden at Bonn. Each individual was covered separately with muslin. No flowers were allowed to expand under cover with those to be crossed, and the latter were emasculated before dehiscence of the anthers.

Reciprocal unions between *inermis* and either of the armed types gave very similar results. From various matings 29 plants were raised, and all bore armed fruits, not one in more than 2000 harvested being destitute of spines or tubercles. There appeared to be a considerable degree of sterility, for the total number of cross-breds represented an average of less than one individual from each mating. Details of the crosses are given below :—

Parentage.	Number of offspring.	
	With armed fruits.	With unarmed fruits.
Inermis A × *tuberculatus* 1	1	None
,, D × ,, 1	1	,,
,, D × ,, 6	2	,,
,, D × type plant	4	,,
Tuberculatus 1 × *inermis* C	8	,,
,, 4 × ,, C	8	,,
,, 5 × ,, C	4	,,
,, 6 × ,, C	1	,,
Total................	29	

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* 'Mém. Acad. Stanisl.,' 1864, p. 214; also 'Flore de Lorraine,' éd. 2, 1857, t. 1, p. 22.

† Suard, "Catalogue des Plantes vasculaires du département de la Meurthe," in 'Statistique historique et administrative,' by H. Lapage, Nancy, 1843, 1re partie, p. 142.

‡ 'B. Z.,' 1884, Bd. 42, p. 243.

In the case of the union between *inermis* and the type form, the fruits of the cross-breds were indistinguishable from those of the armed parent, the carpels being furnished with numerous spines, often hooked, and of varying size, the largest measuring as much as $\frac{1}{8}$th of an inch. In the matings between *inermis* and *tuberculatus* the resulting fruits were intermediate between those of *tuberculatus* and the type form ; numerous spines were present as well as tubercles, but the degree of prickliness was a little less than in the previous case. We have then in unions between the unarmed and the two armed races, in the one case dominance of, and in the other imperfect reversion to the type (spined) form, in both cases the unarmed character is recessive.

Now Hoffmann's results were as follows : from two matings of type (*muricatus*) × *inermis*, dominance of type form (three plants) ; from three reciprocal matings dominance again in one case (two plants), and in each of the two others the appearance of the recessive form (one plant). Hoffmann remarks that the result in these two latter cases may be due either to reversion to the mother form or to unobserved fertilisation. Our own experiments indicate that the latter interpretation is probably correct.

PEAS (*Pisum sativum*).

(Experiments made by W. BATESON and MISS KILLBY.)

Though Mendel's results have been amply confirmed by Tschermak and Correns, experiments with *Pisum* were made partly from a desire to witness the classical phenomena and partly in the hope of elucidating certain obscure points. Tschermak's second and third papers, which have appeared since we began Peas, have provided much information on several of these points, and our work is thus largely confirmatory of his. In addition we have investigated the peculiarities of cotyledon colour in types which, like Telephone, are often piebald, and we are able to add some facts on the properties of "indent" types. Experiments were made to test whether geitonogamy has any effect in weakening dominance. On this point our results were entirely negative, and it seems clear that no such effect is produced.

Cases of irregularity in dominance seemed also worth investigating, and the possibility that departures from the expected F_2 ratios might not be purely fortuitous, was a special subject of inquiry.

The occurrence of degenerate "rogues" among high-class Peas raises important problems in variation and heredity, and experiments on the subject are in progress.

The net result of our work tends to the conclusion that Mendelian principles in regard to heredity in Peas are capable of an application more literal than at first seemed likely. Difficulties based on the supposed variability of the seed characters in the type have proved to be small, and it is doubtful whether there are any genuine "exceptions" which cannot be traced to interference of conditions or mistakes.

Crossing began in 1901. This season was good, and 1902, in which most of the F_1 plants ripened, was fairly good at first, though later the weather broke, and harvesting of late sorts had to be done in the wet. The summer of 1903 began with late frosts in May and June, and was the wettest on record. Total loss of the crop was expected by English growers, and badly coloured samples were common.

In such a season the colour is dull and the seed-characters indeterminate.

The Pure Types.

The first supply was selected from a fine set of samples kindly sent by Messrs. Vilmorin, Andrieux and Co. Others were afterwards obtained from various sources, chiefly from Messrs. Sutton and Sons. I take this opportunity of expressing my thanks to Mr. Arthur Sutton for much assistance, and especially for opportunities of studying several types on a large scale.

In the course of the work much information about these various types was obtained which cannot be included here. N. de B. is very similar to Buchsbaum used by Tschermak. It exists in the *sans parchemin* form as *nain hâtif Breton.* Some types exist in both pointed and stumpy forms, *e.g.*, Perpetual (ptd.) and Continuity (stp.). "Round" applied to seeds does not mean that the seeds are spherical but that they are smooth. F. B., for instance, is squared by pressure.

THE CHARACTERS AND THEIR BEHAVIOUR ON CROSSING.

Cotyledon Colours.

Peas are often classified on their appearance as white or yellow, blue, green, grey. The appearances may be due to the colour of the cotyledons, or of the skins, or both, and therefore such a classification must be used cautiously. The *cotyledon colour* taken alone may present a variety of colours, as follows:—

(1) *Yellow*, as in N. de B., Serp., Sabre, B. Q., Purp., etc.

(2) *Green* as in F. B., B. P., L.'s A., etc. Among the yellows Purp. is perhaps the deepest, and among the greens, perhaps B. P. is the deepest green, but practically the true yellows and greens may be regarded as two uniform types.

(3) *Piebald, tinged or yellowed*, as American Wonder, William I, and Telephone.

Name.	Abbreviation.	Seed-characters.			Height in feet.	Pods.	Flower colour.	Notes.
		Cotyledons.		Skin.				
		Colour	Shape.					
Très nain de Bretagne	N. de B.	y.	rd.	wh., tpt.	dwf., 2½—3	stp.	White	Seed v. small; cots. sometimes greenish.
Serpette nain blanc ..	Serp.	y.	wr.	wh., opaque	dwf., 1½—2½	ptd.	,,	Skin has brown spots in pits, often bursts here.
Blue Peter	B. P.	g.	rd.	tpt.	dwf., about 3	stp.	,,	Often bursts.
Fillbasket	F. B.	g.	rd.	Green, opaque	½ dwf., 3½—4¼	ptd.	,,	Seeds squared by pressure.
Sabre	—	y.	rd.	Greenish, tpt.	Tall, about 5	stp. (?)	,,	Shape of pods unique, curving to suture-side.
Express	Exp.	g.	rd.	tpt.	Tall, 3¾—5½	stp.	,,	Height irregular, but always "*tall*" in habit.
Victoria (marrow) ...	Vict.	y.	rd.	wh., tpt.	Tall, 5—6	stp.	,,	Very late; seeds often pitted.
Laxton's Alpha.......	L.'s A.	g.	wr.	tpt.	,,	ptd.	,,	Cots. rather liable to tinge.
British Queen.......	B. Q.	y.	wr.	wh.-greenish	Tall, 5—7½	stp.	,,	Very late.
Telephone	Tph.	g. tinges	wr.	g. tinges	Tall, 5—6	ptd.	,,	Seeds usually turn picbald or yellow unless protected.
Early Giant	E. G.	y.	wr.	wh.-greenish, opaque	Tall, 5—5½	ptd.	,,	
Purple Sugar Pea....	Purp.	y.	ind.	gr.-br. purple spots	Tall, 6—7	s. par.	Purple	Skin-colour irregular; axils purple.
Debarbieux	Deb.	y.	Flat, smooth	—	½ dwf., 3—3¾	s. par.	White	Size of seeds irregular.
"Irish" Mummy	Irish	y.	rd.	Maple	Tall, 6—7	stp.	Salmon	Fasciated top of stem, stand. wh., wgs. pale red, axils red.
Field Pea..........	F. P.	y.	ind.	Green-brown	Tall, 5—6	stp.	Purple	Seed skin darkens with age, with faint traces of purple spots.
Maple..............	—	y.	rd.	Maple	,,	stp.	,,	

y., yellow; g., green; rd., round; wr., wrinkled; ind., indented; tpt., transparent; dwf., dwarf; stp., stumpy end; ptd., pointed end; s. par., *sans parchemin:* all pods inflated except s. par. sorts. All with coloured flowers have dark axils. Salmon flowers go with red, purple flowers with purple axils.

Uniformity of Types: the Piebald Seeds.

In a fine year samples of yellows or greens picked from healthy plants as soon as the pods are ripe are very uniform in colour. The difficulties which Professor Weldon has suggested may arise from variability, are not commonly experienced. If, however, the weather is bad, certain yellows (*e.g.* N. de B.) are liable to give some greenish seeds; and some of the greens (especially L.'s A.) will always give a proportion of piebald with even a few yellow seeds if the pods are left on the plant till all are ripe.

Two kinds of impure colours have, therefore, to be considered. (1) Yellows which have remained greenish; (2) Greens which have become tinged with yellow. In neither case did selection of the discoloured seeds have the slightest effect on the colour of the offspring, and the evidence strongly indicates that the departure from type is in each case produced by external influences; (1) being due to failure to ripen properly, (2) to bleaching after ripening.

In this connection the normally piebald types are important. Before trial I supposed, with Professor Weldon, that such peas were really "mosaics" of yellow and green, and I, therefore, hoped that they could be used to elucidate the inheritance of a mosaic character. This proved to be a mistake, and the piebald types are evidently green Peas, which are peculiarly liable to tinge. The difference is not due to a mosaicism of yellow and green characters (in the sense in which, for instance, a Carnation may be a mosaic of colour and whiteness), but to the peculiar instability of the green pigment in these types.

All Peas, of course, are green before ripening. Yellow varieties turn yellow *before they are hard.* Piebald varieties, however, may be still green *after they are hard*, and have—in wrinkled types—assumed the wrinkled form. If then gathered, and put in a dark and dry place, they, for the most part, stay green, but if exposed to the light they quickly tinge *on the exposed surface.*

All green Peas will tinge if exposed to the sunlight, especially when freshly gathered, but the piebald types change with much greater rapidity than the ordinary green types. Exposure to moisture has a similar effect. In piebald types, though the older pods contain piebald or even yellow seeds, those in the younger pods on the same plants are still green, though hard. The discoloration is much delayed if the pods are picked, and left unopened.

Another indication of the same kind is the fact that if piebald seeds are examined in the pods it will be found that those in one pod are tinged on *the same surface.* Examination *in situ* frequently shows that the tinging is towards that surface of the pod which is most exposed to weather, and especially to the sun.

The facts here given regarding types commonly piebald hold also for the exceptional piebald seeds of green types, and their departure from the normal green is a direct result of external causes, partly, and perhaps entirely, preventible.

It is, however, true that the degree of susceptibility varies from type to type, and it is possible there may be some variation in this respect between individuals, but no clear positive evidence to this effect was obtained. There is a notable difference between tinged seeds of normally piebald types and those of normally green types, in the fact that while the former germinate as well as green seeds of the same type, the latter show a marked loss of vitality. Tinged seeds of Laxton's Alpha, for instance, though they germinate well enough, if sown at once, scarcely produce any plants if kept till the following March, and those that do grow are feeble. If the seeds are taken up and examined, after being in the ground about 20 days, they are found to be half rotten, and infested with dipterous larvæ, and there is little doubt that the tinging indicates partial death of the tissue. Tinged seeds of Blue Peter were less seriously affected by tinging, and a March sowing of tinged seeds gave plants as good as those from green seeds. In the following year, however, the tinged seeds were dead, though the green ones were still able to germinate freely. This special vitality may be connected with the fact that in Blue Peter the green colour extends deep into the cotyledon, while in Laxton's Alpha, for instance, it is shallower.

In all cases tinged seeds that did grow gave plants with no more tinged seeds than any others of the same type. Numerous experiments were made on these points, which are not worth recording in detail.

The occurrence of tinging, sometimes so complete as to make the seed pass for yellow, is the origin of the numerous statements as to the great "variability" of Telephone in cotyledon-colour. I have seen a sample of Telephone consisting of a great majority of piebald seeds, some greens and some "yellows"; but all sown, even the yellowest, gave the true Telephone type, viz., green seeds liable to tinge after hardening. Another sample, in addition to the above sorts, contained one genuine yellow, which bore yellow seeds only, and behaved as a pure yellow in crosses made with it.* The belief, therefore, that both yellows and greens may each give the other arises from neglect of the distinction between natural yellows, and yellows produced by tinging. Separate harvesting makes this clear at once.

In some varieties (*e.g.*, Sutton's Nonpareil), true yellow cotyledons are about as common as green ones, a clear proof that the original plant selected for the type was heterozygous in this respect. These various facts show how necessary it is in experiments with such types to number each plant used in crossing, and to examine its seeds when ripe in order to be sure that it came true to type. We have next to consider whether the susceptibility to tinging indicates failure of segregation. If so, we should regard the piebald types as in a neutral state between yellow and green.

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* Doubtless a stray.

Experimental evidence, as far as it goes, is quite unfavourable to this view.

When the yellow types ripen, the green colour is changed to yellow, and the same occurs when the piebald types assume the parti-coloured condition; but though the processes may be thus similar it is unlikely that they are identical, and it is almost certain that the latter change is not merely an incomplete manifestation of the phenomenon which is completed in yellow types. It is interesting to note that of the few recorded cases of failure in dominance of yellow most have occurred when Telephone was used. To Tschermak's cases I am able to add the following: Nain de Bretagne × Telephone, giving 4 distinctly green* though slightly yellowish seeds (*v. infra*), the only exception of the kind we have seen. Such a coincidence can scarcely be purely fortuitous, and though the exceptions are rare and irregular, I think they may be taken as indicating a real peculiarity in the piebald type. But in any case since the departure from the normal result, is in the direction of *green*, such evidence is opposed to the view that Telephone's qualities are due to a share of yellowness.

Until the chemistry of these colour-changes is investigated further discussion is hardly possible.

Generally, however, crosses between yellow types and piebald give a normal yellow F_1. In F_2 I have not found the greens less sharply defined from the yellows than when pure green types are used. Crosses between green types and piebald in our experiments gave green F_1, but in some cases many tinged seeds occurred in F_2 mixed with greens, and it was clear that the instability of the green of Telephone had reappeared. Whether segregation of this character (liability to tinging), occurred or not, cannot be stated until F_3 is grown.

Crosses between two *green* varieties gave F_1 seeds distinctly tinged with yellow four times. I supposed, at first, that there might be a case of heterozygous reversion, but the fact that the yellowest failed to germinate at all, and that only three out of nine grew, showed rather that the tinging here also was a morbid change. Those that did grow gave normal greens.

SEED-SKINS.

There are many types of skins, differing in thickness, opacity, and pigmentation. The last is an important character for our purposes.

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* These seeds, however, gave a normal Mendelian F_2. Another similar cross gave 1 yellow F_1, and a reciprocal gave 4 yellow. Nain de Bretagne, as stated

Some coats are practically unpigmented and transparent. (Exp., L.'s A., N. de B.). Of pigmented skins there are four chief types :—

(1) Yellowish- or greenish-white (Serp., B. Q.).

(2) Green, deep (F. B.), or pale (Telephone). The green skins, like the green cotyledons, may bleach on ripening, especially in sorts liable to go piebald. Fillbasket rarely bleaches.

(3) "Greys," namely dull green to brick-red (purple flowered Sugar Peas), usually with a variable amount of purple specks which are obliterated in the redder skins. The redness is merely a matter of exposure to sun in ripening, or to moisture. It is often unilateral. In dull years scarcely any go red, except those that have got wet and are decaying on the surface. The colour gets browner with age. They are called "grey" from the colour after boiling.

(4) "Maples" (*perdrix*), viz., bright brown anastomosing lines and patches of pigment on yellowish ground, always associated with coloured flowers, either purple or salmon, according to the type.

Yellow cotyledons are not often in green skins but occasionally they are.

The skins are important, first, in connection with the phenomenon of "Xenia," viz., a change in a maternal tissue—here the skin—when foreign pollen is introduced. The genuineness of the phenomenon has been questioned, but though capricious it is not rare. It can only be seen when the skin of the seed parent contains a pigment which *can* be transformed. Non-pigmented skins show no xenia. White-skinned seeds sometimes are slightly greenish in crossed seeds, but this cannot be held to be xenia unless it be proved that the change is not merely an arrest of development due to interference.

If, however, a green-skinned Pea with green cotyledons be fertilised with pollen of a yellow cotyledoned type, xenia is often seen in the change of skin colour from green to yellow, associated with the similar change of the enclosed cotyledons. Sometimes, however, the skin does not change and it is pretty clear that, for the effect to be produced, the conditions (presumably the degree of moisture), must be exactly right. I have had excellent cases of xenia in Fillbasket and in green Telephone when fertilized by yellow types.

In grey Peas size and number of purple specks may vary considerably both from plant to plant and from pod to pod.*

The general uniformity of seeds in each pod is striking, and raises the important question whether there is actual differentiation between pods on the same plant.

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above, not rarely gives greenish seeds like Buchsbaum, a very similar type which provided some of Tschermak's exceptions. It is not impossible that the greenness in F_1 was due to bad ripening consequent on the operation.

* Hence the apparent increase in purple spotting in the skins of artificially crossed seeds cannot confidently be attributed to xenia (see later).

The influence of exposure is, however, so great, that it is difficult to know how much of this apparent differentiation is really due to difference of conditions. Correns has expressed the view that in cross-bred plants (from a "grey" parent), the differentiation indicates some failure of dominance, but I have been unable as yet to find greater differentiation between pods on cross-bred plants than on the pure-bred, and I am disposed to think that difference of conditions is the chief and probably the only factor to which such differentiation is due.

As regards dominance, crosses between "greys" and all other sorts except maple show ordinary dominance of "grey." Transparent skins crossed with opaque green or white skins give various results, but never, so far as I have seen, a really opaque skin. The heterozygote skin may be fully transparent, or to some extent, pigmented, and then intermediate in character; but as Telephone and Fillbasket were the only opaque greens used, no general statement can be confidently made. It should, however, be understood that the opacity of skin is too indefinite a character for these purposes. Crosses between two opaque skins gave opaque skins always.

Maple skins gave some valuable results. Laxton crossed Ringleader (skin, from descriptions, white or faintly greenish), with maple, and the F_1 skins were either maple (doubtless with minute purple specks), or various shades of *full purple.* In subsequent generations he describes complex results, amongst others, the occurrence of some *white*-skinned seeds on purple-flowered plants. If the description is correct this would indicate very remarkable segregation of pods. To investigate the question we crossed (1902) maple with Nain de Bretagne, British Queen, and Victoria Marrow, all yellow in cotyledon and whitish yellow in skins (British Queen opaque, the others nearly transparent). Ringleader was not available. The first two crosses bore seeds in F_1 (1903), having skins *maple with purple specks.* Neither parent has any definite purple specks,* though maple has purple flowers and purple marks in axils. This, therefore, is a case of a new and probably reversionary character appearing in heterozygosis. The F_1 skins from the Victoria Marrow cross were plain maples, with no more purple spotting than maple, showing ordinary dominance only. The maple ♀ was the same which, with another ♂, gave full purple spots.

Tschermak records similar purple spotting in F_1 skins from several crosses† made between certain unspotted types of *Pisum arvense* and ordinary Peas with colourless skins, especially Victoria, by Dr. Tedin at the Svalöf Station, and interprets them, no doubt rightly, as examples of reversion on crossing.

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* Minute examination has shown very small spots in occasional maple seeds, which are faint indications of purple specks.

† Correns has also seen a similar case. Tschermak has found the same phenomenon in *Phaseolus.*

The purple spotting was curiously specific in its occurrence, and seems to be a property of certain matings. (For details, see the original.) Two cases are especially noteworthy in which Victoria, used as *mother*, gave with two unspotted types *P. arvense*, purple-spotted F_1 skins, while the skins of the reciprocal crosses were without the purple spots. Our case of maple ♀ × Victoria ♂ similarly gave no strong purple spots. As it is most important to determine the relation of dominance to reversion, it is to be hoped that these cases may be further investigated in order to decide whether the difference between the cases is due to properties of the individuals or of the types.

In 1901 a cross was made between ♀ purple Sugar-Pea (skin "grey" with purple specks) and a form of maple known as the "Irish" pea ("mummy" habit, salmon-flowered, round seeds and maple skins). F_1 skins, 1902, were maple with purple specks, showing simultaneous presence of both parental characters. There were four such plants. One of them, near the top of the plant, bore a few pods with *deep purple* seed-skins like those described by Laxton. In some pods all skins were purple; in two pods normal and purple were both present; one skin was half purple and half maple, with purple specks. A preliminary sowing of these two sorts of seeds was made. Qualitatively, F_2 plants had skins of four kinds: (1) "Grey," viz., brownish, with purple specks; (2) maple with purple specks; (3) maple; (4) in one plant, no mapling, and purple specks no stronger than in maple. F_2 plants from purple F_1 skins did not differ in any way from the rest. One pod only (on F_2) contained three maple seeds *with purple skins.* The number of plants in each class was not recorded, but in view of the result, the case will now be followed up. The maple and purple pigments are in different layers and must be of distinct physiological origin. The allelomorphs must be maple, non-maple, purple, non-purple; and the plant (4) presumably represents the two negatives. (*Cp.* cases of white in F_2 from sap-colour × cream in Sweet-Pea, p. 86, and Stocks, p. 27.) In view of the result with colourless skins, the possibility that the purple specking may be reversionary, must also be remembered in classifying F_2, etc.

Tschermak also obtained several of the full-purple-skinned seeds from Express × Graue Riesen. They were distributed sporadically (as in Laxton's cases and in our own). Of sixteen sown by him, only one gave a plant bearing some purple-skinned seeds, which were again sporadically distributed, some pods containing only such deep purples, others containing normal purple-specked seeds.

Tschermak's experiment proves that the maple character is not essential to the production of the fully purple skins. The evidence, as a whole, seems to indicate that the occurrence of such skins is due to some special conditions and not to any transmissible character. The distribution on the plants proves that it is not merely due to heterozygosis, as I had previously supposed. Nevertheless, the condition is, I believe, never seen in pure-bred purple-specked seeds, and an increase, generally slight, in purple specking is not rare in crosses from such types. I found that the purple colour is easily extracted by boiling, and the normal maple markings are then apparent *and normal.*

Shape and Size of Seeds.

These two characters are not readily separable. Shape is made up of at least two factors, of which the chief is evidently the state of the reserve material. Peas are readily classified as follows:—

(1) *Round*, viz., cotyledons smooth, as Express, Nain de Bretagne, Victoria Marrow, Blue Peter, Fillbasket.

(2) *Indent*, cotyledons with rounded depressions, as the purple Sugar Pea (*Graue Riesen*) and Field Pea.

(3) *Wrinkled*, cotyledons irregularly corrugated, as Laxton's Alpha, Serpette Nain Blanc, Telephone, Veitch's Perfection.

Many kinds (*e.g.*, William the First) contain a mixture of round seeds, intermediates between round and wrinkled, and apparently fully wrinkled. But just as in the case of colour, piebalds are not really intermediate between yellow and green, so here it is found that in these mixed types the wrinkling is spurious. Mr. R. P. Gregory* has shown that the starch grains in round and indent Peas are large, and in wrinkled Peas very small, and frequently compound. "Intermediates" have starch of the "round" type, and it is doubtful whether any genuine intermediate exists. The same is true of the apparent intermediates seen in F_2, which also are of the spurious kind. These are spoken of as "pitted" seeds.

Indent Peas have peculiar properties, and must be carefully distinguished from both sorts. Confusion has already arisen from neglect of this distinction. Their starch is of the "round" type. The chemical nature of these differences is still unknown, though possibly conversion has taken place in the starch of wrinkled types.†

Pitted seeds may occur in any round type, but are specially common in some, *e.g.*, Victoria. When they occur *they are generally associated in pods.* Selection of such seeds does not usually lead to any departure from type, and there is no doubt that, as a rule at least, the change is due to conditions.* Occasionally, especially in a bad season, there is so much pitting that F_2 seeds cannot be sorted without histological examination.†

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* 'New Phytologist,' vol. 2, 1903, p. 226.

† Denaiffe ('Pois Potagers,' p. 8) points out that at the same stage of maturity, before they shrink, wrinkled types contain a much greater proportion of water than round ones, and conversely that when dry they can take up much more water than the round. To the former fact is of course due the fact that wrinkled Peas are still tender at a stage when the round are hardening.

Wrinkled seeds show an almost absolute uniformity, apart from the question of rogues and sporting.

Round × round always gave round F_1, and wrinkled × wrinkled always gave wrinkled F_1. In crosses between round and wrinkled, no genuine exception to dominance of round occurred. Cases of slight dimpling occurred, but these gave ordinary Mendelian F_2. In one case all seeds were wrinkled, but these proved to be self-fertilised.

Indent Peas, fertilised by wrinkled types, do not change their shape, but wrinkled, fertilised by indent, give a *round* F_1. F_2 from both such crosses consists of indents and wrinkleds (mixed in the pods just as in ordinary F_2 from round × wrinkled), doubtless as 3 : 1, but as the difference between the types is rather elusory, the classification cannot be exactly made. Wrinkled seeds, selected from F_2, gave pure wrinkled F_3.

Indent × round gives indent F_1, and round × indent gives round F_1. The shape, therefore, is here, though an embryonic feature, decided by the maternal plant just as much as the seed-coat. *All F_2 seeds from* BOTH *these crosses are, nevertheless, indent*, showing indent as a dominant character (similarly "maternal"). In F_3, however, some plants have exclusively indent, and some have exclusively round seeds, showing the reappearance of the round—here recessive—character as a maternal property. The meaning of this peculiarity is not obvious, but it must not be confused with difference between reciprocals. The statistical proportions are presumably the normal 3 : 1, but, as only sample sowings were made to test the qualitative result, no statement as to the ratio can be made.

Our results also with maple and indent are practically the same, *mutatis mutandis*, as Tschermak's on Graue Riesen (indent) crossed with several white-flowered round sorts. In all these cases he got uniform (indent) F_2 seeds, while these F_2 plants bore F_3 seeds, either indent or round, without mixture on individual plants. Just as in Laxton's experiment, *the round seeds were peculiar to white-flowered plants*, and consequently were in unpigmented (strictly "non-grey") skins, while the indents were all on purple-flowered plants in "grey" skins.‡

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* The existence of such a type as William I shows that liability to pitting must sometimes be a transmissible character; but even then it is very irregular, and clearly dependent on conditions.

† It is presumably to such appearances that Mendel refers when he says that weakly plants often give uncertain results; and unless the pods be examined separately, great confusion may be introduced by such cases, and numerous contradictory observations might be made.

‡ [Fillb. × purple sugar has since behaved similarly. The statement (Mendel's Principles, p. 156) that Debarbieux × behaves thus is incorrect. It was based on

Similarly, in our case, all the round F_3 seeds were in maple skins, *without* purple spots; but the indents had *either* maple-purple-spotted skins, *or* spotted skins without maple marks. No mixture of these seed or skin-characters was seen on any plant, and Laxton's observation of such segregation *by pods* is as yet unconfirmed.

Tschermak's use of "*schwach gerunzelte*," in application to indents, has led to the supposition that the character "wrinkledness," is here dominant over round; but the fact that indent must be distinguished from both is abundantly clear, especially in the results of crossing indents with a genuine wrinkled type.

In connection with the reversionary appearance of purple spots in the skins, Tschermak observed on several occasions seeds which are described as *wrinkled* in F_2 (borne by F_1 plants), resulting from some of his crosses between various *arvense* forms and Victoria. As he interprets this also as reversionary, like the spotting, "wrinkled" may be presumed here also to mean *indent*, and not *pitted*. We have not seen this interesting result in our crosses, and the only cases in which it could conceivably have occurred, were those of Maple × Victoria or × Nain de Bretagne. In both these cases F_2 seeds were round.

There are several features of shape that would require much space for adequate treatment. It is likely, also, that certain types, both of round and wrinkled, have other peculiar physiological properties, which ought to be carefully examined. To these only a bare reference can be made. The most striking concerns the difference between what may be roughly called *small* and *large* seeds. There are round and wrinkled of both sorts. Generally speaking, when large and small are crossed, the size of F_2 seeds is intermediate, but I have seen a case suggesting segregation in these characters.* When a large wrinkled green, like Telephone, is crossed with a small round yellow, like Nain de Bretagne, the green wrinkleds in F_2 are not in the least like the original Telephone, being smaller and quite different in shape. Mr. R. H. Lock, crossing a small round native Pea at Peradeniya (Ceylon) with Telephone, has seen a similar result, and, as he pointed out to me (*in litt.*), "shape" cannot be treated as *one* character, but may depend on a combination of many. In all such cases, the wrinkled seeds, for instance in F_2, have a general resemblance to each other, showing again a peculiarity of shape as a maternal character, comparable with that seen in indent Peas. There cannot be any doubt that, when the F_3 seeds are formed, the Telephone shape will reappear as characteristic of individual *plants*.

In most types and cross-breds, individual *pods* sometimes occur, which contain only *very small* uniform seeds, about half the normal size. This

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F_1 appearances, but F_2 proved that nothing abnormal occurred. In all abnormal *Pisum* cases, a *dark* seed-skin is present. Note, February, 1905.]

* The next generation (F_3) was unfortunately lost.

phenomenon is met with also in Sweet Peas. It has nothing to do with crowding, as the pod is almost empty and flat, though of the usual length and width. When two pods are on one peduncle, I believe it is always the case that, if either contains such small seeds, both do.* No cause can be suggested for this phenomenon. There is no appearance of unhealthiness in the pod or the peduncle. The occurrence is frequent on thoroughly fine plants. These curious "small" seeds did not germinate less well than normal ones, and they produced perfectly normal plants of good size, with normal seeds.

Shape of Pod.

Mendel found the hard pod, with a tough lining membrane, dominant over the *sans parchemin*, or *sugar-pod*, which is without such a membrane. Our experience has been that, though pods of F_1 are never *sans parchemin*, they are decidedly less hard than the hard type, and might sometimes be almost described as intermediate in character. F_2 showed the normal segregation, with the exception of a single plant, which bore pods, some of which would pass for inflated, while others were of the constricted type. Unfortunately, the development of the "parchment" was not examined in this case.

There is great diversity in the shapes characterising the pods of various types, but they may be roughly classified into those known as "stumpy," which, when the pod is full, have a blunt rounded end, and those which are *pointed*. We have found the former always dominant over the latter, and F_2 segregates normally. This observation of the dominance of the stumpy over the pointed types is in agreement with the similar results obtained by Tschermak, and will almost certainly prove to be of wide general application, and of value to the practical breeder.

Height.

This character is liable to considerable fluctuations, which in great measure are due to conditions, especially to difference in preparing the soil, manure, season, etc. Injury to the cotyledons or to the young plant has a marked effect on the height.† The tall types, moreover, are probably not really "pure" in respect of height, but might be subdivided into "*reine Linien*."‡

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* In all cases of noticeable peculiarities distinguishing the seeds of individual pods, paired pods are generally alike in their peculiarity, whether of colour, shape, or size.

† Experiments on this question have been made by Dimon, 'Biol. Bull.,' vol. 2, 1901, p. 209.

‡ *Cf.* Johannsen, 'Erblichkeit in Populationen und in reinen Linien,' Jena, 1903.

Hence it is clear that height is not a character well-suited to these experiments, and reliable results can only be got when extreme types are used.

Peas are usually classified as tall, half-dwarf, and dwarf, and though plants occur of all intermediate heights, the terms are fairly distinctive and easy to apply.

Dwarf Peas range from about 1 to 3 feet;
Half-dwarf, about 4 feet;
Tall, about 5 feet and upwards.

The distinction between tall and the rest is a definite one, and it would scarcely be possible to hesitate as to whether a plant belongs to the tall class from the time it is 6 inches high. At this stage, when rapid elongation begins, the talls form relatively long internodes, beginning from about the 4th or 5th. The stem also in the dwarfs and half-dwarfs bends stiffly at each node, forming a zigzag, while the talls are much straighter and more flexible. In talls, moreover, the root is much longer. These distinctions in habit are almost more characteristic of the classes than the actual heights.

The distinction between the dwarfs and half-dwarfs is not nearly so sharp as between them and the talls. The heights of the types taken here in almost every case greatly exceeded those given in the books for these types, being sometimes double. Our plants were grown singly, well manured, and measured on the stretch when growth had ceased. The indications in the books, I imagine, refer to the heights of the plants, sown in drills, at the time of cropping. Many types, especially dwarfs, when mature, have the lower part of the stem more or less horizontal, and this would not be reckoned in stating the height for cultural purposes.

The position of the lowest flower is independent of the height, but is fairly constant in each type.*

The absolute height and the position of the first flower are liable to show deviations if the seedlings are injured by birds, or otherwise, and I have little doubt that the chief irregularities in the direction of reduction in height are all due to this cause. No tall type ever gave a plant which could be mistaken for a half-dwarf, nor did the latter ever give a tall, with the exception of a single plant in a row of Eureka, a variety not used in these crosses.

Of all crosses between talls and dwarfs or half-dwarfs, none presented the dwarf habit. In one case (Serpette × Express) two plants were raised which were much shorter than the reciprocals, but they were noted as weakly plants, and they had none of the dwarf character. I attribute their shortness to some unhealthiness or injury. The same applies to three plants from Laxton's Alpha × Serpette. With the exception of a few cases of this kind, F_1 plants were tall, and frequently much taller than their tall parent. The increased height of the heterozygotes was most marked in Laxton's Alpha × Blue Peter, and in crosses with the purple Sugar-Pea.

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* Economically this character is important, because low flowers, beginning at about the 7th node, indicate precocity, while high flowers, beginning at about the 12th to 20th nodes, indicate lateness. It is difficult to count the nodes with absolute accuracy. Many records on this character were made, but are omitted to save space. Crosses between low flower and high flower often give an F_1 intermediate in this respect, but definite dominance of very high flower and extreme lateness was also seen (*e.g.*, British Queen).

Crosses between dwarfs and half-dwarfs gave commonly an intermediate result as regards height, and in all cases the characteristic zig-zag habit was retained. No tall plants came from such crosses.

The 1903 sowings suffered greatly from the late frosts, and several lots were much injured by birds. The Telephone crosses were more attacked than any others, and the irregularity in their heights is without doubt due to this cause. Many of them were completely destroyed, and some of those which grew had every leaf picked off in April.

Importance would attach to the question whether half-dwarf segregates from dwarf, as the case is typical of many natural phenomena of heredity. No sufficient opportunity of testing the point has occurred, for an exceptionally favourable season and uniform conditions would be needed in order to study such small differences. Such evidence as exists is slightly in favour of non-segregation. [*Note added February*, 1905. In 1904 a striking case of intensification of dwarfness was seen. Fillb. (half-dwf.) × purple sugar (v. tall) gave F_2 8 tall, 2 half-dwf., 2 extreme dwf.]

The Order of F_2 Seeds in the Pods.

Great labour was devoted to the solution of this question, and many plants were mapped throughout in the hope of detecting an order in the distribution of the seeds. Numerous crosses of F_1 plants with pure recessives were made for the same purpose. No regularity, however, was found. The presumption that some order exists is so strong, *à priori*, that I am disposed to think that the process of oögenesis in which the dominant or recessive character of the egg-cell is determined must be liable to disturbance by accidents.

The Nature of "Rogues."

Even under careful selection, occasional "rogues," or untrue plants appear, and their existence constitutes a most important problem. With Mr. Arthur Sutton's help I have begun to investigate this question, and though little has so far been discovered, the matter must be alluded to as bearing on the question of purity of strain.

Rogues may occur in any type, but are much commoner in some than in others. Some of these are merely recurring recessives and call for no discussion, but a certain number are *dominants* appearing in recessive strains. Of these, many are traceable to imperfect selection of the type-seeds. For instance, in Veitch's Perfection a round rogue is very common. This is primarily due to *pitted* seeds of the rogue passing for *wrinkled* seeds of the type.

On minute inspection such seeds can be recognised. They give the usual round seeded rogue, and I find this is an ordinary dominant when crossed with the type.

The question then arises whether *all* rogues are similarly due to imperfect sorting, or to recurrence of recessives, but the balance of evidence is scarcely favourable to this view.

Some rogues are so primitive in habit that it is very unlikely they can be recessive, and their seeds are sometimes so characteristic that it is almost impossible they can get passed over in the fairly rigorous hand-picking to which Peas are subjected. We are, therefore, in all probability, here confronted with a problem of original variation. To investigate it the seeds of individual plants must be separately sown on a large scale, and the attention of experimenters is called to this attractive inquiry. The first question is to decide whether the wild rogues are given off by a few plants only, as seems likely, and if so, to determine their distribution on these parent plants.

If it appears that the rogues are merely recurring recessives, or due to imperfect sorting, it should be possible to get rid of them once for all.

Wiegmann ('Bastarderz. im Pflanzenreiche,' 1828, p. 14) states that he saw a natural cross between *Pisum* and *Vicia*. Such a statement needs confirmation. I have seen but one case of a suspected natural cross on *Pisum*, and I incline to think it was a pod which I had myself crossed, and omitted to label.

NUMERICAL RESULTS (F_2 seeds).

Table I.—Yellow and Green.

No.	♀.	♂.	Height in feet.	Yell.	Green.	Dubious.
			Wrinkled.			
17*a*, 1	L.'s A.	Serp.	About 7	77	26	2
2			,,	84	21	
3			,,	116	28	
4			,,	57	21	
5			,,	138	44	
17*b*, 1	,,	,,	$6\frac{3}{4}$	96	31	
2			6	56	17	
3			$6\frac{1}{2}$	90	33	

Table I.—Yellow and Green—*contd.*

No.	♀.	♂.	Height in feet.	Yell.	Green.	Dubious.
12, 1	L.'s A.	Serp.	5	Lost		
2			6¾	76	22	
3			5¼	51	16	7
13, 1	,,	,,	3	19	7	
2			4¼	20	8	1
3			7	67	18	2
4			4¼	4	2	
17*c*, 1	Serp.	L.'s A.	4½	47	9	2
2			5½	42	16	
3			5¼	60	9	
23, 1	Teleph.	E. Gt.	4	19	5	
2			4¼	26	11	
3			4	23	7	
24, 1	E. Gt.	Teleph.	3¾	15	10	
2			5½	53	22	
25, 1—3 mixed.	,,	,,	3	31	10	3
Round.						
14, 1	Vict.	F.B.	7	141	46	
2			7	93	38	
3			6¾	138	53	
4			5 +	77	32	
5			6½	58	16	3
29*a*, 1	F. B.	Deb.	4—4½	298	79	
2			,,	10	2	
3			,,	163	66	3
29*b*, 1	,,	,,	4¾	173	72	2
2			4	107	35	
31*a*, 1	,,	N. de B.	3¾	111	41	
2			,,	69	21	
3			,,	145	44	
4			,,	197	64	
5			,,	91	30	
6			,,	162	54	
31*b*, 1	,,	,,	3½	67	24	1
2			,,	97	36	1
3			,,	70	14	8
4			,,	49	25	2
+ Loose seeds.				16	7	
2, 1	,,	,,	Not recorded.	31	15	1
2				92	34	2
3				77	29	1

Table I.—Yellow and Green—*contd.*

No.	♀.	♂.	Height in feet.	Yell.	Green.	Dubious.
K1, 1	F. B.	N. de B.	1¾—3 ft. (17 plants being 2—2½).	40	12	
2				8	1	+*
3				8	1	+
4				4	2	
5				13	6	+
6				35	13	
K2, 1	”	”		15	2	+
2				27	20	+
3				9	3	+
4				7	5	+
5				35	13	
6				44	16	+
K3, 1	”	”		65	14	+
2				12	2	
3				18	5	
4				19	5	+
5				10	4	
K4, 1	”	”	2—2½	15	5	+
2			”	13	7	
5, 1	N. de B.	F. B.	3	111	46	3
2			2¾	69	18	3
3			2¼	23	12	
37, 1	B. P.	Deb.	3¾	55	24	
2			4	32	20	1
K5, 1	Sabre	Exp.	2¾—5¼ (9 being between 4 and 5 ft.).	70	27	
2				44	16	
3				13	2	
4				81	26	2
5				100	32	
6				75	29	
7				34	4	
K6, 1	”	”		24	14	
2				95	37	
3				12	4	3
4				13	6	
5				49	17	
6				83	20	
7				41	13	
K7, 1	Exp.	Sabre	5¾	74	32	
2			6¾	89	24	
		Total	....	5321	1804	

Ratio, 2·95 : 1

* + means many seeds shed before gathering.

Table II.—Round and Wrinkled.

	Green.					
No.	♀.	♂.	Height in feet.	Round.	Wrinkled.	Dubious.
18*a*	L.'s A.	Exp.	5	73	20	5
K8, 1	,,	,,	about 3	32	9	+
2			,,	30	10	
18*b*, 1	Exp.	L.'s A.	5½	70	28	
2			4¼	28	7	
3			3½	14	2	
4			4¾	67	17	
5			5	73	25	
18*c*, 1	,,	,,	6	81	28	1
2			5½	46	14	
3			5	40	12	
4			3¾	34	11	
18*d*, 1	,,	,,	about 6	88	20	
2			,,	60	28	1
3			,,	114	46	1
4			,,	102	38	
5			,,	61	15	
18*e*, 1	,,	,,	about 7	95	37	
2			,,	87	40	
3			,,	53	19	1
4			,,	69	25	5
5			,,	76	33	1
6			,,	40	9	
K9, 1	,,	,,	about 4	18	6	+
2			,,	21	6	+
3			,,	21	9	+
19, 1	L.'s A.	B. P.	6	104	28	
2			7	134	35	
3			7¼	96	21	2
4			6½	107	32	
K10	,,	,,	Tall	23	6	
20*b*, 1	,,	F. B.	7	88	21	
2			7½	70	29	
3			6½	26	11	
4			7½	67	14	+ ?
*20*c*, 1	F. B.	L.'s A.	7	39	18	
3			8¼	79	37	
4			8½	78	31	
5			9	120	40	
6			8¼	98	39	

* 20*c*, 2 proved to be self-fertilised.

Table II.—Round and Wrinkled—*contd.*

No.	♀.	♂.	Height. in feet.	Round.	Wrinkled.	Dubious.
27, 1	Deb.	Serp.	$2\frac{1}{2}$	6	1	
2			4		Lost	
3			$3\frac{1}{4}$	25	6	1
4				30	9	4
5				57	26	
*35, 1	B. Q.	N. de B.	about $6\frac{1}{4}$	253	92	15
2			,,	108	22	2
3	(a branch only)		,,	50	13	3
4			,,	151	45	
K11, 1	Serp.	Sabre	$3\frac{1}{2}$	32	12	
2			4	16	2	
3			$4\frac{1}{4}$	38	8	
K12, 1	,,	N. de B.	$2—2\frac{1}{2}$	42	14	
2			,,	49	15	
3			,,	6	0	
4			,,	16	9	+
5			,,	70	24	
18, 1—5	F. B.	Teleph.		332	119	25
19, 1	,,	,,	7	55	22	4
2			$6\frac{3}{4}$	66	24	2
3			5	69	20	
20, 1	,,	,,	$4\frac{1}{2}$	23	9	3
2			$4\frac{1}{4}$	4	2	
28	,,	,,	5	32	9	1
21	Exp.	,,	$7\frac{1}{2}$	94†	29	6
		Total	....	4246	1408	
				Ratio, 3·02 : 1		

Table III.—Yellow Wrinkled and Green Round.

No.	♀.	♂.	Height in feet.	yr.	yw.	gr.	gw.	Dubious.
16*a*, 1	Serp.	Exp.	$2\frac{3}{4}$	20	10	6	2	
2			$3\frac{3}{4}$	21	9	11	4	
16*b*, 1	Exp.	Serp.	$6\frac{1}{2}$	96	37	28	6	34‡
2			$6\frac{1}{4}$	70	17	15	5	2
3			$5\frac{3}{4}$	69	19	27	3	2
4			$6\frac{1}{4}$	131	45	44	9	13
5			6 +	83	32	24	8	11
6			$5\frac{3}{4}$	74	33	23	10	6

* 1 proves to be self-fertilised.

† Much pitting.

‡ Shapes doubtful: 24 y., 10 g.

Table III.—Yellow Wrinkled and Green Round—*contd.*

No.	♀.	♂.	Height in feet.	yr.	yw.	gr.	gw.	Dubious.
16*c*, 1	Exp.	Serp.		110	45	37	19	3
2				52	12	17	3	1
3				83	26	11	11	5
16*d*, 1	,,	,,	4	58	13	29	5	1
2			5	79	23	25	10	4
3			5	41	11	10	2	
4			5	65	13	26	4	1
5			6¼	56	15	11	3	16
7	,,	,,	about 3¼	16	9	7	1	2
8			5¼	42	11	12	5	4
11, 1	,,	,,	5	49	20	16	10	7
2			2	11	3	7	1	
3			5			lost		
9, 1—3	,,	,,		94	31	26	15	14
32*a*, 1	F. B.	,,*	3½	142	40	48	7	19
32*b*, 1	,,	,,	3—3½	53	19	20	7	4
2			,,	53	18	28	2	7
3			,,	85	23	27	5	8
4			,,	54	12	26	10	3
5			,,	53	22	13	7	3
32*c*, 1	,,	,,	,,	16	10	7	1	
2			4	65	20	28	10	8
3			4	98	35	38	10	1
4			4¼	87	36	25	10	2
5			3¾	18	2	5	2	2
6			4¼	74	27	30	9	5 +
7			4¼	91	33	42	9	5
32*d*, 1	,,	,,	about 4	67	23	27	2	1
2			,,	80	23	21	6	9
3			,,	62	23	21	5	11
4			,,	68	17	18	6	
5			,,	45	24	15	1	6
6			,,	47	14	12	1	1
7			,,	77	17	26	10	4
32*e*, 1	,,	,,	,,	98	40	29	4	2
2			,,	55	13	11	6	1
3			,,	76	23	19	9	17
4			,,	38	18	16	3	1
5			,,	67	22	23	7	4
6			,,	75	30	15	6	

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* This combination gave a very uniform height.

Table III.—Yellow Wrinkled and Green Round—*contd.*

No.	♀.	♂.	Height in feet.	yr.	yw.	gr.	gw.	Dubious.	
32*f*, 1	F. B.	Serp.	$3\frac{1}{2}$	61	27	18	4	3	
2			,,	107	26	20	9	6	
3			,,	82	27	23	7	7	
1, 1	,,	,,	$3\frac{1}{4}$	70	24	30	6	2	
2			$3\frac{1}{2}$	175	65	68	21	13	
3			,,	32	8	14	2	9	
4			,,	37	23	13	9	3	
30, 1	,,	Tph. yell.	$3\frac{1}{2}$	17	6	6	2	1	V. poor.
2			$3\frac{3}{4}$	12	4	4	0	3	
3			,,	8	6	3	0		
34, 1	B. P.	Serp.	$2\frac{1}{2}$	27	11	8	0		
2			,,	34	6	11	4		
3			$2\frac{3}{4}$	40	7	11	1		
4, 1	Serp.	B. P.*		42	16	17	9	2	
2				77	27	28	5		
3				53	21	16	4		
4				37	12	11	4		
Yellow Round and Green Wrinkled.									
15† 1	N. de B.	Teleph.	6	50	13	17	4	7	
2			$6\frac{1}{2}$	75	18	14	7	6	
3			$6\frac{1}{2}$	31	11	12	3	20	
17	,,	,,	7	60	22	31	8	6	
29, 1	Teleph.	N. de B.	4	28	8	14	4	1	
2			5	24	6	4	2	3	
3			3	6	2	2	0		
K13, 1	Sabre	L.'s A.	4 ft. 10 in. to 6 ft. 3 in.	88	44	37	7		
2				25	11	10	1		
3				14	8	8	0		
4				74	21	16	5	1	
K14, 1	,,	,,		22	16	4	2	2	
2				74	18	29	4		
3				47	21	12	5	2	
4				71	28	18	12		
5				85	23	31	8		
6				18	8	8	4		
7				47	19	16	7		
8				52	14	13	7	1	
K15, 1	L.'s A.	Sabre		19	0	10	2		
2				15	6	4	3		
3				26	5	8	5		
Total ...				4926	1656	1621	478		

* Tinging and pitting.

† In this case the F_1 seeds were greenish (p. 60).

Taking the whole mass of seed results in F_2, involving one pair of allelomorphs, there were :—

5321 yellow, 1804 green, giving the ratio	2·95 : 1
4246 round, 1408 wrinkled ,, ,, ...	3·02 : 1,

where 3·0 is expected. The ratios found in individual plants, 62 for shape and 85 for colour, are not enough for full discussion, and a study of them does not, so far, suggest the presence of any definite disturbing factor.

In the seed-results where two pairs of allelomorphs, shape and colour, are considered, the totals are :—

rd. yell.	wr. yell.	rd. green.	wr. green.
4926	1656	1621	478
4878	*1626*	*1626*	*542*

the expectation being shown in italics. The deficiency of wrinkled green is noticeable. Of the seeds classed as "dubious" (generally exclusive of dead seeds) the majority could be sorted either as regards shape or colour, but these details are not worth printing. The case of 16 *b*1, is interesting, as in it there were 34 seeds (24 y, 10 g), which could not be sorted with confidence in regard to *shape*. They were mostly the produce of certain pods which contained exclusively "pitted" seeds. As stated above, this appearance is due to some unknown somatic disturbance, and has nothing to do with transmission. The net deficiency of green wrinkled seeds is probably due to a slightly greater tendency to tinge, or to burst, owing to which a larger proportion have been consigned to the "dubious" class, or have been rejected as dead.

Various F_2 green seeds and wrinkled seeds were sown and gave exclusively recessive seeds, nothing new being observed. Particular attention was paid to these tests in the case of F_2 from crosses with the Purple Sugar Pea × a wrinkled green (L.'s A.), the case not having been investigated before. The behaviour of the recessive was normal throughout. The dominants were DD or DR as usual.

The statements as to the behaviour of the coloured-flowered types in their crosses are founded on the following original crosses and their descendants :—

	Pods.	Seeds.
L.'s A. × Purp.	1	4
Recip.	1	5
Exp. × Purp.	1	5
B. P. × ,, ...	1	6
Deb. × ,, ...	1	1
Purp. × N. de B.	2	10
,, × Irish	1	4

	Pods.	Seeds.
Purp. × F. B.	1	6
,, × Teleph.	1	1
Recip.	1	2
Teleph. × F. P.	1	7
Maple × Purp.	1	1
,, × Vict.	1	8
,, × B. Q.	1	5
,, × N. de B.	2	7
,, × B. Q.	1	6
Recip.	2	10
Purp. × Sabre	3	16
Recip.	3	16
B. Q. × Purp.	2	7

Correct F_2 numbers for seed-colour could not be given without peeling, or for shape without sowing. There is no reason to suppose that they are of special interest. As explained, the *plant* characters of F_2, etc., are important, and these will be followed up.

Summary of Evidence on Peas.

The evidence, for the most part, is confirmatory of that of Mendel and others. The following points are noteworthy.

1. F_1 from tall × dwarf or × half-dwarf was always tall, often greatly exceeding the original "tall" in height, but from dwarf × half-dwarf it is usually intermediate, and was never tall. The character, height, is liable to great fluctuations, largely due to conditions and injury, perhaps also to mixture of types. "Tall" segregates from dwarf, as is well known, but it is not yet certain that half-dwarf segregates from dwarf.

2. *Seed Characters* (*a*) *Colour.*—Tinged and piebald cotyledons must not be treated as genetic characters "intermediate" between yellow and green, nor are they mosaics. The yellow in them results from external conditions, being sometimes morbid, sometimes natural. Susceptibility to such changes in some green types is common, in others rare. To dominance of yellow one dubious exception was seen, which, nevertheless, gave a normal F_2.

(*b*) *Shape.*—"Round" was always dominant over "wrinkled." "Indent" is quite distinct from "wrinkled" and from "round." Crossed with wrinkled, the indent type behaves as round. Crossed with round it behaves as a maternal or *plant* character, being dominant in F_1 plants. In gametogenesis it segregates from round, but indent can only appear in association with a coloured seed-coat (and flowers). On the other hand "round" though segregated cannot appear in the seeds borne by F_1. A similar case has been seen by Mr. R. H. Biffen.

When Polish wheat is crossed with Rivet, the F_2 seeds are of intermediate length, though doubtless the F_2 plants will bear respectively long, intermediate, and short seeds.*

True wrinkling is always associated with, and probably depends on a peculiar condition of the reserve materials, of which the small and compound starch grains are the visible indication (Gregory). From this the pitting and spurious wrinkling, sometimes common in round types and in F_2 from crosses, must be distinguished. Spurious wrinkling is evidently due to conditions, though special susceptibility to it is probably transmissible (*cf.* William I, p. 65). Nevertheless, no difference could be seen in the offspring of extremes in this variety.

(*c*) *Seed-coat.*—Greys and browns associated with coloured flower are always dominant. Crossed with whites they occasionally *give "reversionary" F_1 with purple spots*, though neither parent has such spots. The deep purple coat occasionally seen on such seeds is probably due to conditions and has not been seen to be transmitted.

3. The common application of the term "variable" to the shapes and colours of Peas rests on a misconception. No case of variation in either respect has been observed, which has borne critical investigation. The statement that variation occurs in these characters is founded on observation of somatic differences, or on results of crossing misunderstood. There is no evidence that the colour or the shape can be changed by selecting these somatic differences.

On the other hand, at various points of time, such variations must have taken place; the green has arisen from the yellow, and the wrinkled from the round. There is no reason for supposing that these changes were due to progressive selection, and it is practically certain that they were discontinuous. Whether the "rogues" now occurring in many types are true variations is uncertain. Many of them certainly are not, others possibly are.

4. *Exceptions.*—Writing, in 1902, I was disposed to believe that genuine exceptions to the dominance of yellow cotyledons or of roundness, and to the purity of segregation of these allelomorphs from their recessives, might be not infrequent. Experience has shown that such exceptions are in any case very rare, and it is doubtful whether there are any which cannot be referred either to mistakes or to interference of external conditions.

We are probably right in declaring that when true yellow is crossed with true green, or true smooth cotyledons with true wrinkled, yellow and smooth are always dominant if the external conditions are the same.†

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* Now described in full; Biffen, 'Jour. Agr. Sci.,' I., 1905.

† [Since this was written, Tschermak has given further details ('Zt. landw. Versuchsw., 1904') of cases giving exceptional results after F_2. It is conceivable that a true anomaly of segregation was involved in some of these, but it seems

5. All the characters studied are independent and separately transferable, with the following exceptions. Flower colour and axil colour and "grey" or "maple" seed-coat are not usually separable, but Tschermak has seen a form with flowers coloured and axils plain.

Indent shape seems to be inseparable from the seed-coats proper to coloured flowers. It may nevertheless segregate, both from round shape and from wrinkled.

SWEET PEA (*Lathyrus odoratus*).

(Experiments carried out by W. Bateson, E. R. Saunders, and R. C. Punnett (in 1904).)*

Types of Pollen.

After the the re-discovery of Mendel's work it seemed desirable to use varieties differing in a pollen-character. Searching for such forms, it was found in October, 1900, that the Sweet Pea, Emily Henderson (referred to as E. H.), a pure white var., usually has pollen distinct from that of normal vars. When dry it is irregularly kidney-shaped or *round*, while normal pollen is long with straight sides. Treated with reagents normal pollen swells to an *elliptical* shape with a distinct long axis, and shows *three* pores set evenly round the short circumference. Round pollen thus treated becomes nearly *spherical*, and usually has only *two* pores. These pores are sometimes placed at two poles, but not rarely are asymmetrically placed, in which case one may be larger than the other. Grains with only *one* pore occur in round pollen. In E. H. these are rare, but in some of the later derivatives they may be fairly common, and even constituted the majority in a few plants. Lastly, grains which, though round, are three-pored, are not very uncommon.

Extensive search among plants of many natural orders has revealed no similar case. Variation in number of pores is not rare, *e.g.*, in some Violas and Tropæolum, where two-pored and even one-pored grains may occur among the normal three-pored, but no variety was found characterised by an abnormal pollen.†

more likely that the results were due to misleading appearances of various kinds. February, 1905.]

* We are indebted to Miss Hart-Davies and Mr. Keeble for growing and recording part of the F_2 crop at Reading, and much assistance has been given by Messrs. Doncaster, Balls, Wood, and others in recording the Cambridge crop.

† Perhaps *Fuchsia procumbens* is a case of this sort. It is said to be two-pored, while other species are three-pored. We have not yet had this species in flower (see Masters, 'Gard. Chron.,' 1874, p. 291). In 1904 it was noticed that *Medicago echinata*, "Calvary clover," has four-pored pollen, apparently as a normal feature, though all other species examined were three-pored. January, 1905.

The round pollen was discovered in a short row of E. H., sown without any thought of experiment, which had survived into late autumn. Seed of this row was collected promiscuously, the importance of the subject not being realised. In 1901, when experiments were contemplated, this seed was examined, and it was found to contain some *black*-skinned seeds mixed with the drab or *light*-skinned seeds proper to all truly white varieties. The *black* seeds proved that at least one of the original row had been a coloured plant. But since the seed came from a Sweet-Pea specialist, all blacks would certainly have been picked out from the seed supplied. Therefore it is certain that the coloured plant or plants were "rogues," *i.e.*, offspring of a white or normal mother-plant. The nature of such rogues we shall presently discuss.

Besides the home-grown seed, other samples of E. H. were obtained from various firms. These were all found to give, together with "round" plants, a variable number, which, though otherwise identical with E. H., had normal *long* pollen. Such longs are usually a minority, but samples have been seen in which longs were as common as round.

With the exception of E. H. the ordinary tall varieties of Sweet Peas are apparently all long-pollened, but among the dwarf procumbent varieties called *Cupids*, rounds are common, white Cupids in particular being almost always round.

The half-dwarf or "bush" variety, known as Mont Blanc or New Early White also frequently has round pollen. Both this and white Cupid are very like E. H. in other respects, and there is every probability that they were derived directly from it.*

In 1901, a large number of crosses were made between the long and round E. H. and between each of them and certain coloured types. Of these, many failed, but a good number of F_1 plants were produced.

In all F_1 plants the pollen is long, and experience has shown that the characters long and round generally behave as Mendelian dominant and recessive plant-characters.

Mixed Pollens.—Round grains are never found on "long" plants, and never occurred in F_1. But in subsequent generations an apparently genuine mixture of characteristic long grains among pollen otherwise round, was seen in occasional plants, and was proved to occur even in individual anthers. These "mixed" plants may have amounted to about 2 per cent. of later generations, and sometimes were associated in particular families. Such mixture must be distinguished from the occurrence of three-pored round grains in normal round pollen. The true mixture is not only rare but very capricious in occurrence, and plants showing mixture in an occasional flower may have in most flowers only round pollen. As the mixed cannot be certainly distinguished from the round, they are all counted together for the present as round.

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* As one grows familiar with pollens, other classes become recognisable in addition to round and longs. For the present such further subdivision is not attempted. With practice it is likely that some types at least could be recognised by their pollens.

Rounds, being recessive in that character, give, left to nature, rounds only, except for an occasional "rogue" such as may occur in any type. Seed from many putative "mixed" plants was saved, but in only one case (offspring of a "rogue") did a distinct proportion of longs appear (14 long, 52 round), which were not merely "rogues."

Longs, with the rarest exceptions (which are probably due to error, see p. 92), give either longs only, or longs and rounds approaching the ratio 3 : 1.

Before experiment it seemed just possible that F_1 would visibly exhibit the underlying gametic differentiation, as a mixture of longs and rounds, but the evidence so far is very decidedly against this view, and it is certain that such mixture, though having doubtless a distinct significance, is a very rare and exceptional phenomenon.

Our evidence indicates that the shape of the pollen grain and the number of pores is a zygotic and not a gametic character, just as seed-coat is. Mr. R. P. Gregory has made careful studies of the maturation-processes in various types, but, so far, has found no difference between the pollen-formation in long and round.

The pollen-characters having—with a few exceptions—a simple Mendelian behaviour, the importance of the work relates almost entirely to colour-inheritance, but before introducing this subject two other structural characters may be referred to.

Cupids.—These are dwarf procumbent plants, making no erect stem. Their leaves are a peculiar dark green. They behave as simple recessives. F_1 from Cupid × tall is tall. F_2 gives 3 tall : 1 Cupid. The actual numbers seen were 693 tall, 215 Cupids, or 3·22 : 1. Cupids left to Nature give, as a rule, Cupids only. An exception to this was seen at Messrs. Sutton's, in the fact that Cupids Mme. Carnot (blue), F_3 from white Cupid × Mme. Carnot, gave 2 white Cupid, 24 Cupid Mme. Carnot, *and* 12 *tall blue-purples.* There can be little doubt that these latter were due to crossing by *Megachile* (see "rogues," p. 95). In 1904 they gave normal F_2 families.

Cupids are difficult to seed. They not rarely have deficiency of pollen, and, consequently, must be very liable to get crossed. Moreover, they often amputate their flowers at the pedicel-joint. Other types do this sometimes, a whole plant being occasionally thus affected. Probably this also is a recessive character. Cupids frequently have round pollen, and there is little doubt that the white Cupid, one of the first Cupids—if not the first—came as a mutation from E. H. The other Cupids have been obtained by crossing Cupid with various tall types, of which most of the best known are now to be had as Cupids.

The Cupid habit can thus be combined in F_2, or later, with any previously existing colour, according to the ordinary Mendelian principles.

"*Snapdragon*" *Types.*—In these the standard is tucked in, forming a hood, like the flower of *Linaria.* This is a recessive character. F_1 has standard erect, or very slightly hooded, like the hooded types (*e.g.*, Blanche Burpee). F_2 gives 3 erect : 1 "snapdragon." Numbers observed erect, 246; "snapdragon," 77; or 3·02 : 1.

It is nearly certain that the hooding of ordinary hooded types is a similar recessive, though actual counts have not been made. Though in F_2 the segregation of the "snapdragon" character from the erect standard is complete, an intermediate state is possible.

Salvation Lassie is almost exactly intermediate between a true "snapdragon" such as Red Riding Hood, and the type. The fact, here well illustrated, that an intermediate type may, on occasion, come into existence (whether by mutation or crossing), though the two extremes habitually segregate, is one of great theoretical significance.

[Attention is called to the "Snapdragon" types as good subjects for experiments demanding a plant practically above suspicion of any possibility of crossing by insects.]

Colour.

Through the great kindness of Messrs. Sutton and Sons we have been permitted to study, year by year, the long series of Sweet Pea crosses made by them. This privilege has been most valuable, enabling us to make acquaintance with the phenomena of heredity in Sweet Peas on an ample scale, and to direct our own experiments in the light of the experience gained at Reading. We take this opportunity of acknowledging our great indebtedness to Messrs. Sutton and their staff for the constant help they have afforded us in placing their crops and records in the freest way at our disposal.

At the present time there are more than a hundred colour-types in Sweet Peas. The colours are of two kinds: (1) those due to cell-sap colour, ranging through chocolate, purple, blue, red, pink; (2) yellow, due to presence of coloured plastids, here spoken of as *cream;* or to various combinations of (1) and (2).

Besides flower-colour the plants may differ in colour of axils, which are either red, here called dark axil (*dk. ax.*), or simply green, here called light axil (*lt. ax.*).

The phenomena are greatly complicated by the occurrence of reversion, and various processes of resolution and disintegration; but, speaking generally, white is a recessive to sap-colour, cream is recessive to non-cream, and lt. ax. to dk. ax. Therefore, cream is always homozygous. White × any sap-coloured type has, so far, always given a reversionary F_1 (excepting 1 case of magenta self "Her Majesty"), and white by white has always given reversionary F_1 when "pure" parents, with long and round pollen respectively, were used.* The results from pure-bred cream types, without sap-colour, crossed with white are not yet known. Crosses between two sap-coloured types give complex results and are only referred to incidentally in this paper.

The reversionary F_1 may present one of two forms. It may either revert totally to the original *purple* type, or it may be the *red bicolor* known as Painted Lady (P. L.). The two are never mixed together in F_1 families. The axils may or may not revert to the dark type.

The wild purple type is common in Sicily, and through Dr. S. F. Harmer we have received valuable information respecting it from Professor Gojacono and Mr. Whitaker, who have most kindly sent a dried flower. This agrees exactly with the ordinary purple F_1. Professor Gojacono also tells us that the red bicolor is occasionally found wild, but he has never seen a white wild. The P. L. form is also stated to have been originally brought into cultivation from Ceylon.†

The purple is still sometimes grown as "Purple Invincible." The P. L. is grown under several names, each type presenting slight differences chiefly in tint of wings, ranging to magenta, when it is known as "Miss Hunt." An early type, "Earliest of All" × Mont Blanc, round, gave ordinary dominance with a fairly simple Mendelian F_2 (about 40 P.L. various tints and 11 white + 2 purple "rogues"), seen at Messrs. Sutton's.

The existence of two reversionary types, the one a total, the other a "half" reversion, is important, and leads to various complications.

CROSSES (F_1).

So far in our crosses white *long* × coloured has given purple F_1; and white *round* × red *sap-coloured* has given P. L., but × blue sap-coloured gives purple.

White long × white round sometimes gives purple, sometimes P. L. No F_1 family ever contained a mixture of these, but the factors which decide whether the reversion is total, or half, are still unknown.

Purple F_1 presents various minor differences according to the coloured type used, some having blue, others purple wings. A form flaked with red-purple occasionally appears, and once F_1 was striped with white something like "Grey Friar."

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* Extracted whites have a different behaviour.

† *Cf.* Burmann, 'Thes. Zeylanicus." This is clearly Painted Lady, but as Trimen mentions no Lathyrus in his 'Flora of Ceylon,' there is grave doubt as to the original record. Mr. R. H. Lock, as the result of inquiries made at Peradeniya, writes that he can hear of no such plant native in Ceylon.

Similarly the F_1 P. L. ranges from the common form with white or pale pink wings to Miss Hunt, and in this respect individuals may differ in the same family. Considerable differences in these minor respects may occur between flowers on the same plant. Late flowers are often flaked and irregular in colour.

The following list shows the evidence as to F_1 obtained in 1901 and 1902 (put together to save space. Of course the former only have reached F_2). As reciprocals have hitherto been alike, they also are not distinguished from each other.

pur., purple ; pk., pink ; cr., cream ; choc., chocolate ; td. wh., tinged white ; wh., white.

	Parents.	F_1.	Families.
I.	*White long × white round—*		
	E. H. long and round	29 pur. dk. ax.	9
	„ „	1 P. L. dk. ax	1
	Blanche Burpee × E. H. red......	3 pur. dk. ax.	2
	„ „ „	14 P. L. lt. ax.	3
II.	*Whites of similar pollen—*		
	E. H. round × ditto	3 wh. rd.	3
	Bl. Burpee × E. H. long	9 wh. long	3
III.	*White long × cream—*		
	E. H. long × cream long	3 pur. dk. ax.	1

(The cream was saved from an extracted F_2 cream, proved pure on selfing, giving about 200 cream + 1 P. L. and 1 white, regarded as rogues.)

IV. *White long × red sap-colour, with or without cream.*

The following types were used. The first figure gives the number of plants, the second the number of families. F_1 purple, unless otherwise stated. All dk. ax.

Venus, pk. cr., 1, (1) ; Her Majesty, 1, (1) : Lovely, pk., 24, (7) ; Queen Victoria, pk. tinged, cr., 13, (4) ; Lottie Hutchins, flaked pink 1 F_1, striped pur. ; Salopian, red, 1 ; Gorgeous, red cr., 1 ; F. Bouverie, pk., 3 (1) ; Sadie Burpee, black-seeded, tinged wh., 7 (2) ; Firefly, red, 17·1, (3) ; Lady Penzance, pk., 1.

In above cases, E. H. long was the white parent. In addition Bl. Burpee white long × Sadie Burpee black-seeded, tinged white, gave 1 purple. Once Bl. Burpee ♀ × Mrs. Sankey ♂, very like Sadie Burpee used in last cross, gave 3 *whites*, but these, being quite exceptional, are for the present suspected of being accidental self-fertilisations.

V. *White long* × *blue or purple sap-colour.*

E. H. long × Navy Blue, peculiar clear blue, lt. ax., gave 3 dark purple, slightly dk. ax. (1); Black Knight (choc. purple) × E. H. long gave 5 purple dk. ax. (1).

VI. *White round* (*E. H.*) × *red sap-coloured, with or without cream.*

F_1 was P. L. in all cases.

Venus, pk. cr., 13, (6); Queen Victoria, tinged cream, 15, (3); Sadie Burpee, tinged wh., 1; Prince of Wales, carmine, 4, (1); Firefly and Mars, reds, not distinguished, 27, (6); Lady Penzance, pk., 5, (2);

VII. *White round* (*E. H.*) × *blue or purple sap-coloured.*

F_1 purple in all cases.

Navy Blue, blue, lt. ax., 2 lt. ax., (1); Black Knight, choc.-purple, 4 (1); Countess Cadogan, blue-purple, 7 dk. ax. (1); Stanley, rather irregular, purple to choc.-purple, 1; Countess Radnor, lavender, 2, (1).

In some of the above crosses there is reversion to dark axil, but in others, reversion in flower-colour occurs without any change to dark axil.

F_2.

Except in the case of simple dominance given above (p. 84), F_2 results are all complex and cannot be fully understood till F_3 and F_4 are grown. In all cases of reversion a more or less numerous series of new types appears in F_2. Generally speaking (from white × sap-colour), white reappears in the proportion of 1 white to 3 sap-coloured (actually 379 to 1245, 1 : 3·29).

In one family, Venus × E. H. rd., two F_2 gave *no* white (in 64 F_2 plants). The evidence points to some mistake having been made in that case, and suggests that these plants were really DD in sap-colour. These 64 are omitted from total. Nevertheless there were certain distinct irregularities when Venus was used, and it is not impossible that some of these effects may be really due to monolepsis or to failure of segregation. As cream is recessive to non-cream, *untinged* creams must be added to the whites and this is done in total given.

At Messrs. Sutton's cases were seen of the appearance of true *whites* in F_2 from Mrs. Eckford (a pure cream with light axils and seed-skin), crossed with three different coloured types, viz., Her Majesty (magenta), Countess Radnor (lavender), and Queen of Pinks (pink, ? with cream). Mrs. Eckford is a pure cream, viz., a white + coloured plastids. A similar appearance of whites occurred in Stocks (see p. 27), and evidently is due to recombination of the characters no sap-colour with uncoloured plastids, according to the ordinary scheme for di-hybrids. The only difficulty lies in the case of Queen of Pinks, which *looks* as if it had coloured plastids. Presumably this appearance is misleading. Mrs. Eckford × Queen Victoria (tinged cream) of course gives no whites in F_2, for both parents have cream.

The coloured offspring in F_2 are generally capable of being classified and sorted into types without much difficulty, though, from the fact that the nature of cream was not understood when the work began, some want of uniformity was introduced. The following is a list of the types which constantly recur :—

	Standard.	Wings.
(1) *Purple*.........	Choc.-purple.	Blue, or purple.
(2) *Picotee*.........	White edged with purple or red.	White edged with blue.
(3) *Painted Lady.*	Red.	White to pink.

This ranges to Miss Hunt, which has magenta wings, from which it cannot be always distinguished.

(4) *Tinged white.*—White with faint red tinge, especially at base of standard.

As picotee flowers fade the standard becomes suffused with red,* and may then be easily mistaken for P. L., though the buds distinguish the two at once, picotee being whitish, while P. L. is red. P. L. and tinged white, on the contrary, grow paler with age. The latter is a much diluted P. L., standing to it much as picotee does to purple.

The following also occur in certain matings :—

(5) *Her Majesty.*—Self-magenta.

(6) *Pink P. L.*—A distinct but rather irregular class in which the prevailing colour is pink, not red.

As regards the valency of these colours the evidence so far indicates that—

(1) May contain or be dominant over all
(2) ,, ,, ,, (4) and *white.*
(3) ,, ,, ,, ,,
(4) ,, ,, ,, white only.

It is noticeable that (2) has not, so far, given (3). This evidence, however, has not been derived from actual F_2 plants of known origin, but from specimens of these types raised from "rogues." It is probably a fair indication, nevertheless.†

Where cream has been introduced, all the red types (3), (4), (6) may have cream in addition, and the same is probably true of types (1)

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* Such suffusion on fading is common in picotee varieties, *e.g.*, red picotee tulips, and Shirley Poppies.

† Fully confirmed in 1904.

(2) and (5) also, though in them cream is not so easily detected. The type Queen Victoria, spoken of below, may be regarded as (4) with cream added.

Any of the coloured types may have either dark or light axil; but a genuine white or cream untinged, has a green pedicel, with the axils light (and a pale seed-skin).

Distribution of Pollens in F_2.

When a round pollened parent (P) is used, any F_2 type may have either round or long pollen, but the proportion of long to round individuals differs greatly in different types.

At the present time it is scarcely profitable to suggest gametic formulæ for any of these families. This can only be attempted when F_3 has been grown, and it is known which are homo- and which heterozygous, what types each may contain, etc. In several cases, however, the F_2 statistics make it almost certain that actual flower-colour-bearing gametes of several types may be produced by F_1 plants even when both parents were white, and there is no doubt that gametes bearing dark axil may be produced by the F_1 from two light-axilled types (probably an illustration of the phenomenon seen by Cuénot in mice).

In several cases the numbers indicate that F_1 plants, though own sisters, do not have precisely the same gametic formulæ. This is well seen in the case of E. H. round × E. H. long, where the discrepancies between individual F_2 families were too great to be fortuitous. This fact proves either (1) that there was heterogeneity in the gametes of the original parents, which is very possible; or (2) that the process by which gametic differentiation arises is liable to disturbance; or (3) that irregularities occur in fertilisation. Possibly all these factors contribute to the result, but the chief cause is probably to be sought in (1) and (2).

To settle these questions a great range of observations will be required, and for the present we must be content to deal with the simpler cases. The F_2 families are now given in order, first from a purple F_1, then from a P. L. F_1 (*l.* = long: *r.* = round).

I. FROM F_1 PURPLE.

(1) *From E. H., Long* × *E. H., Round.*
(*White* × *White*).
(9 families).

651 plants flowered in F_2 from 9 F_1 plants. Of these, 14 were imperfectly recorded.* Omitting these, 637 remain.

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* Viz., 1 pur. *l.*, 8 pic. *l.*, 3 P. L. *r.*, axils unrecorded; 1 pur. dk. ax. and 1 white, pollen unrecorded.

Purple	*l.*,	dk. ax.	176	P. L.	*l.*,	dk. ax.	10
		lt. ,,	45			lt. ,,	6
,,	*r.*,	dk. ,,	11	,,	*r.*,	dk. ,,	23
		lt. ,,	2			lt. ,,	17
Picotee	*l.*,	dk. ,,	39	Td. wh.	*l.*,	dk. ,,	2
		lt. ,,	15			lt. ,,	3
,,	*r.*,	dk. ,,	7	,,	*r.*,	dk. ,,	5
		lt. ,,	1			lt. ,,	7
White	*l.*		195				
	r.		73				

Neglecting axils there were 649, with pollens as follows:—

Purple	*l.*	222	or *17·0 : 1*	P. L.	*l.*	16	or *1 : 2·7*
,,	*r.*	13		,,	*r.*	43	
Picotee	*l.*	62	or *7·7 : 1*	Td. wh.	*l.*	5	or *1 : 2·4*
,,	*r.*	8		,,	*r.*	12	
White	*l.*	195	or *2·7 : 1*				
,,	*r.*	73					

The peculiarities of this distribution are without doubt significant. Taken together there are 500 long, 149 round, or 3·36 : 1; and 382 coloured, 269 white, or 1·42 : 1. The last figures indicate some complication.

Since the original parents were both white, the simplest expectation is equality of white and coloured. It is, therefore, almost certain that the excess of coloured is due to production of colour gametes. This, however, cannot have been uniform in all families. An analysis showed that of the 9 F_1, five gave an approach to equality* of white and coloured, and the great excess of coloured was all in four families.

In the purples and picotees *long*-pollened plants are in excess. The facts suggest that of purples about 1 in 16 is round, and of picotees about 1 in 8. But the P. L. and Td. wh. always have *round*-pollened plants in excess, probably as about 3 : 1. *There is, therefore, some coupling of pollen-shape and colours.*

The fundamental question to what extent the colours in F_2 depend on heterozygosis, being as yet unanswered, a full analysis is impossible. Meanwhile, it may be noted that the distribution shows that the gametes cannot be merely whites of two kinds in equal numbers (which might, perhaps, be expected), nor can there be an equality of coloured and white, but the actual composition must be something between these two. It is, moreover, almost certain that one of the coloured gametes is such as to produce picotee and tinged white at least.

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* A similar F_2 family was kindly recorded at Reading by Miss Hart-Davis, but as in it the picotees, P. L., and tinged whites were not distinguished from each other, these numbers are only available for the rougher statistics. In it there were 75 coloured long, 12 coloured round, 63 white long, 29 white round, *i.e.*, 92 coloured, 87 white, or approximate equality; 138 long and 41 round, or 3·3 : 1.

F_1 × Types.—A few matings of purple F_1 with the parental types have been made. These, so far, have given the following totals:—

F_1 with E. H., rd., gave 2 purple, 1 P. L., 2 white, all long,
and 1 P. L., 6 white, all round.

F_1 with E. H., long, gave 6 purple, 4 picotee, 3 white, all long. The details will be given when this part of the work is further advanced.

(2) *From Firefly × E.H., long.*

(*Red × White.*)

Firefly is a red self, axils usually light. It is scarcely if at all distinct from Mars, and the two are not separated here. The purple F_1 is the same as that formed in (I) above, from two whites. Five F_1 gave 299 F_2 plants, 64 white, 235 coloured. To these we can add a family of 140, recorded by Miss Hart-Davies, at Reading, viz., 33 white, 107 coloured; in all, 97 white, 342 coloured, or 1 : 3·5. Of the coloured, 269 were purple, 73 red, or about 7 : 2.

The Cambridge crop was further subdivided as follows:—

Purple	149	*6*	*7*	*9*	*149·4*
Purple to Black Knight	35	*1*			*24·9*
P. L.	29	*1*	*2*		*24·9*
Miss Hunt to Firefly	22	*1*			*24·9*
White	64	*3*			*74·7*

The figures in italics show the ratio that the observed statistics suggest, and the expectation on that ratio. The two classes of purple and the two classes of reds cannot be subdivided with precision. The deficiency of whites is perhaps noteworthy.

A remarkable feature is the *almost total disappearance of Firefly*, and the same occurred (p. 93) in F_2 from the P. L. F_1 of Firefly × E. H., round. Special interest also attaches to the appearance of Black Knight. Intensification of a character, in this case colour, in some members of F_2 not rarely follows a cross with a type destitute of that character—in this case albino.

This phenomenon has played a great part in the evolution of domesticated varieties. We may, perhaps, conjecture that the deep claret Cyclamen, "Vulcan," arose in this way, but this peculiar segregation occurs with other classes of characters also. Where F_1 is P. L., no Black Knight or other purple appears in F_2.*

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* Unless two rogues are so regarded.

Axil.—The axil of the Firefly used was not recorded, but there is scarcely a doubt it was light. F_1 was dark, and of the coloured plants in F_2, 230 were dark, 110 light, in addition to the 97 white.

(3) *E. H., long* × *Lady Penzance.*

(*White* × *Red-pink, Axils light.*)

Appearance of Sterility.—One F_1 only, purple, with purple (*not* blue) wings: axils dark. In F_2, 227 plants; a remarkable family for the reason that it contained a large proportion of plants in which the male organs, at least, were *sterile.* These anthers were in various states of imperfection, some small, others of fair size, but withered, or "contabescent," to use Darwin's term.

The female organs of these plants may have been normal,* for a few seeds formed on some, presumably fertilised by *Megachile.* Artificial fertilisations all failed, but they were made after the bad weather set in, and the fact therefore proves nothing. One plant recorded early in the season as contabescent, afterwards produced both pollen and seeds, and is therefore counted as fertile. No other doubtful plant was found. The presumption seems to be that only the male organs were affected.†

Among the coloured plants the sterility was almost entirely confined to those which had *light* axils. Of 53 sterile plants, 12 were white, and of the 41 coloured, only two had dark axils. Conversely, of 126 coloured and fertile only five had really light axils (including the plant named above), two had axils faintly coloured, and 48 were white.

Altogether there were 173 fertile, 54 sterile, or 3·25 : 1, a ratio which makes it probable that this sterility is a recessive character transmitted in Mendelian fashion.‡

Altogether there were 60 white, 167 coloured, or 1 : 2·78.

The case is of importance in another way. In this, as in some others, the coloured dark axil to coloured light axil are about 3 : 1, excluding the whites. Therefore it is likely that the whites themselves consist of two classes, those which would have dark axils *if the flowers were coloured*, and the rest. Here we should therefore expect fertile, *i.e.*, "potentially" dark axil whites—to be to the sterile whites, *i.e.*, the light axil whites, as 3 : 1. They are as 4 : 1 (48, and 12) which, though somewhat out, indicates clearly enough the existence of the two expected classes. The fact will illustrate the probability that the white in F_2 from such a mating as E. H., long × E. H., round, may again consist of two classes (both in longs and rounds), and that different breeding results may be expected from each. In all likelihood it is to the existence of such differences among albinos that many observed complexities are due.

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* A case of contabescent anthers in *Primula sinensis* had female organs perfectly fertile.

† In 1904 artificial fertilisations of such plants succeeded.

‡ The occurrence of extensive and similar sterility was seen in one other family, which gave 44 fertile, 19 sterile, coloured 49, white 14. The incidence of sterility was almost exactly as in the case given above, the coloured plants with *light* axils being almost all sterile. Unfortunately there was some error in the labelling of this family, and as its origin cannot be given with certainty, we are obliged to neglect it.

Contabescent anthers were seen from time to time in many families, though commonly confined to individual flowers. This sporadic sterility has not been particularly studied.

It is interesting to compare this example of the definite appearance of sterility, at least on the male side, with the familiar occurrence of sterility in cross-breds. Such a phenomenon has often been supposed to indicate remoteness of kinship, yet here a closely comparable effect occurs in F_2 as the result of a cross between two types which must be very nearly related.

Mr. Gregory in a careful examination of the pollen-genesis, found that the divisions were normal up to the reduction-division, when the chromosomes form shapeless knots and entanglements, failing to divide.*

II. FROM F_1 PAINTED LADY (RED AND WHITE).

(1) *From Blanche Burpee × E. H., Round.*

(White × White.)

F_1, ordinary P. L. : axils light, 10 plants.

F_2, 272 plants (of which 41 were raised and recorded at Reading). They were distributed thus :—

Coloured long.	White long.	Coloured round.	White round.
116	83	41	32

This gives 199 long to 73 round, and 157 coloured to 115 white. From these figures it is practically certain that there have been some coloured gametes produced by F_2, but how many and of what kind cannot yet be stated.

The coloured plants were all P. L., ranging to Miss Hunt, except 5 Her Majesty and 3 rogues not reckoned.

In addition to the above, 1 F_1 plant gave at Reading an entirely aberrant result, 53 long, 2 reckoned as round, and 2 uncertain. Until such a result is confirmed we regard it as probably due to some error.

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* 'Roy. Soc. Proc.,' 1904, vol. 73, p. 91.

(2) *From Lady Penzance* × *E. H., round.*

(*Red-pink, Light Axil* × *White.*)

F_1 ordinary Painted Lady, light axils: 5 plants from 2 pods.

172 F_2 plants from 4 F_1 plants, 46 white, 126 coloured, viz., 1 : 2·7. The coloured plants were chiefly Painted Lady (83) and a certain number of pink Painted Lady (23). There were 17 others distributed among various coloured sorts, including 3 picotees (from 1 plant, ?rogues) which are unexpected. Only 1 plant of Lady Penzance appeared.

Result may be summarized thus:—

P. L.	Other colours.	White.
83	43	46

Coloured long.	Coloured round.	White long.	White round.
89	37	36	10
9	*3*	*3*	*1*
96·7	*32·2*	*32·2*	*10.7*

But though grouped thus roughly the result is simple, it must be remembered that undoubtedly several types of colour gametes have arisen, and there are many complexities to be subsequently considered. Lady Penzance is the variety which gave the sterile plants in F_2 from E. H. long (p. 91).

(3) *From Firefly* × *E. H., Round.*

(*Red* × *White.*)

F_1 ordinary P. L. Firefly usually has light axils, but some have dark. In the original parents this point was not noted. Probably one was DR in dark axils, for 4 F_1 from it had dark axils and 2 had light. Axils apart, the families presented no differences, so all are put together.

Of 943 plants 209 were white, 734 coloured, or 1 : 3·51; 205 were round or mixed, 658 long, 1 : 3·2 (rest not done). In this case the "mixed" were comparatively frequent.

The following is a summary of the fully recorded plants:—

Coloured long.	Coloured round.	White long.	White round.
480	144	132	45
9	*3*	*3*	*1*
450	*150*	*150*	*50*

The italic figures show the expectation on the simple hypothesis of 9 : 3 : 3 : 1, and though there is an approach to these numbers it is pretty clear that there is some disturbance not accounted for.

The coloured forms were mostly P. L. (360 long, 122 round), 98 were

Miss Hunt (78 long, 20 round), of which 18 longs were somewhat like the magenta Her Majesty. Only 24 long and 2 round in any way resembled Firefly, and several of these were not very different from ordinary Miss Hunt. Firefly is therefore almost entirely disintegrated.

(4) *From Queen Victoria* × *E. H., Round.*

(*Tinged Cream, Axils Dark* × *White.*)

F_1, 8 plants P. L. (1 with some magenta in wings): all dark axils.

F_2, 270 plants, namely, 38 white, 23 cream without sap-colour, and 209 with sap-colour, of which 89 were creams. As regards pollen the grouping was as follows:—

Coloured sap.		Uncoloured sap.			
		Cream.		White.	
Long.	Round.	Long.	Round.	Long	Round.
151	58	14	9	35	3
209		23		38	
3		61			
202·5		*1*			
		67·5			

Long to round are, therefore, 200 to 70, 2·8 : 1.

Thus far there is great simplicity in the arrangement, but several underlying complications must be noticed. There is an unaccountable scarcity of *round* whites. The whites without cream are only 38, to 23 with cream, where 3 : 1 would naturally be expected. Moreover, the whole number of non-cream is 158, cream being 112, showing that a similar proportion, about 1·5, exists in the whole group.

There was a good deal of overlapping between the colours, and all cream types are somewhat difficult to classify strictly, but the following table shows the proportions approximately. Besides P. L. there appeared a *pink* (quite distinct from the red P. L.), and some of a peculiar pinkish cream resembling "Venus." The numbers suggest that Venus is the pink + cream. Only 7 Queen Victoria came in F_2.

P. L. no cr.		P. L. cr.		pk. P. L.		Near Venus.	
l.	r.	l.	r.	l.	r.	l.	r.
57	28	35	13	31	4	21	13

Q. Vict.		White.		Cream (no tinge).	
l.	r.	l.	r.	l.	r.
7	0	35	3	14	9

(5) *From Venus* × *E. H., Round.*

Venus is pinkish cream of a peculiar shade, axils usually light. The four families which have reached F_2 showed such individual peculiarities (in addition to that described in F_1) that they could only be described at length. Moreover, there is a strong suspicion that the original sample of Venus used contained a mixture. All the E. H., round, used as fathers, were from the same stock of seed, but the number of plants used is not known.

The most aberrant results were seen in the case where F_1 consisted of 3 Miss Hunt (p. 87). Of these, one gave no white and no round in F_2. The second gave 12 white, 36 coloured, but no round. The third gave 37 long, 13 round, but no white. It is scarcely doubtful that some cross-bred was accidentally used as the original father, and that the record is wrong.

The other three families, though each showing peculiarities, have several points in common. Together they gave 283 long, 81 round (3·5 : 1); 267 sap-coloured, 97 uncoloured (12 being cream, 85 white); and the same distribution, 267 non-cream, 97 cream (2·75 : 1). The coloured plants were various reds and pinks, with or without cream, about 50 approaching Venus. In this case it is evident that non-cream behaves as an ordinary dominant to cream.

Behaviour of Extracted Whites.

Investigation of this subject has so far been insufficient, and we have to rely on evidence derived from the use of whites extracted from "rogues." All the facts observed point to the conclusion that extracted whites, whether long or round, give only *white* when bred together. Details will be given when more experiments have been made, but in view of this result, it is conceivable that all the coloured in F_2 from two whites are due to the production of colour-bearing gametes by F_1.

Accidental Cross-Fertilisation: "Rogues."

It is not doubtful that *L. odoratus* is, as a rule, self-fertilised, but the question whether it is ever crossed has been often discussed by Darwin and others. Our experience is that hive-bees and *Bombi* when they visit it, which they do not habitually do, almost always go to the base of the flower, working at the side. The leaf-cutter (*Megachile*), on the contrary, *habitually* visits Sweet Peas, partly for honey, but especially for pollen. This insect settles on the keel, depresses it with the hind legs, and with them scrapes up the pollen off the stigma, plastering it on its abdomen.

This operation obviously gives a risk of crossing.* But as the anthers dehisce before the bud opens, the risk is greatly reduced, for fertilisation is probably begun, if not completed, before the cross can be made. If, however, from any cause the pollen is defective, crossing becomes probable. Such deficiency certainly occurs sometimes. Apart from the want of pollen regularly occurring in certain plants described above, flowers without pollen are from time to time seen on seemingly normal plants. If in these the female parts are perfect, crossing must be expected.

Secondly, careful trials proved that the round pollen of E. H. is not ready to germinate in sugar solution when the flower begins to unfold, an age at which long pollen germinates freely, and it is almost certain, therefore, that these round whites are exceptionally liable to crossing. Our experience has been that "rogues" (purples or P. L.) do occur much more often in round E. H. than in long, and there is a presumption that they are crosses. Mr. Leonard Sutton kindly made inquiry from growers in California, where most of the Sweet Pea seed is raised, but they had no such experience of E. H. It should be remembered, however, that they would be growing many acres of a sort together, and *Megachile* may, perhaps, not occur in that country.

All varieties of Sweet Peas give occasional "rogues," which are often either purples or P. L. On the whole it seems likely that they are all crosses, but the possibility that they are due to more profound causes must be remembered. In our own work F_2 consists partly of plants selfed under cover and partly of seed set exposed. Among the former no unexpected plant has occurred, but among the latter there has been a trifling percentage—about 1 or 2—of plants which can hardly be supposed to be normally produced, *e.g.*, purple in offspring of whites, P. L.'s, or creams.

These were all recorded, but are neglected in this account. A trifling error is doubtless introduced by the presence of an occasional P. L. "rogue" which cannot be recognised as such.

In all crossing it is most important that the pollen should be taken either from an unopened flower or from covered flowers. In fine weather the pollen of open flowers may naturally have been mixed by *Megachile.* This condition latterly has been strictly obeyed, but the necessity was not sufficiently appreciated in the original crosses of 1901.

Summary of Evidence and Discussion of Results in Sweet Peas.

1. The characters "long pollen" and "round pollen" usually behave as ordinary plant characters, being dominant and recessive respec-

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* In some years (*e.g.*, 1903) the minute beetle *Meligethes* abounds in Sweet Pea flowers. It is not known whether it travels from flower to flower, or whether it is capable of crossing. Flowers containing *Meligethes* were not used for fertilisations.

tively. Long grains are occasionally seen on "round" plants, but as yet only one plant bearing round pollen has been found to give any "long" plants on self-fertilisation.

2. White flower-colour is recessive to all sap-colours.

3. The character, coloured plastids, giving a cream-colour, is recessive to absence of colour in the plastids; consequently, cream is recessive to white.

4. Light axil commonly behaves as a simple recessive to dark axil. The figures frequently show that the result 3 dark : 1 light appears in the *coloured* plants alone, whites never having dark axil, thence it might be suggested that there is a correlation or "coupling" between light axil and white. This would pre-suppose an asymmetrical distribution of axil-colours among the gametes. The facts may be more satisfactorily expressed by inverting the conception thus: in order that the dark axil may appear, the allelomorph to which it is potentially due must be introduced into the same zygote as the allelomorph of sap-colour. We should then recognise *two* classes of whites (both long and round), one which contained the dark axil allelomorph and one without it. The very important case of F_2 from Lady Penzance (p. 91), practically proves that this view is correct, for there sterility of the anthers probably indicates the white plants without the dark axil allelomorph. It is not improbable that such a distinction between different whites is a factor, if not the factor, which determines the reversion to purple *or* to Painted Lady. It should not be impossible to test this suggestion experimentally, for the statistics of F_1 from whites in that family should settle the question.

5. In crosses with white, F_1 generally reverts either to the original purple, or to the red bicolour, Painted Lady, which is also known to be a primitive type. The reversion may or may not affect axil-colour. The most striking cases are those in which one or other of these reversions occurs as the result of crossing white, pollen long, with white, pollen round. As yet Painted Lady has only come once as F_1 from the two Hendersons, but the occurrence of purple sometimes and Painted Lady sometimes from Bl. Burpee (white) × E. Henderson, round, proves that two whites, apparently identical, may give either of these reversionary forms—of which one may be called a *whole*, and the other a *half*-reversion.

6. The long E. H. may naturally be supposed to be, in origin at least, an extracted recessive, though, perhaps several generations old. A chance cross on E. H. would give black F_2 seed and this would usually be rejected; but if any of it were sown, white plants might arise and henceforth pass for pure E. H. Such plants would be 3 longs to 1 round.

Nevertheless, the phenomenon of reversion is not much elucidated by this consideration; for the reversion is not to any type with which a cross is likely to have happened, but to one or other of the two primitive types. The evidence from Blanche Burpee, also, is unfavourable to this supposition, for it also gives either purple or P. L. when crossed with E. H., round, while × E. H., long, it has so far given whites only.

7. Though the reversion occurs when the long white is crossed with the round white, it must be remembered that the fact does not prove that it is the meeting of these differences in one zygote which "causes" the reversion. On the contrary, the numbers in F_2 show plainly that there may be *white* heterozygotes of long and round (proved in 1904), and it is almost certain that it is the meeting of some other qualitative differences which determines the reversion.

8. In all the cases where F_1 is reversionary, a complex disintegration and recombination of characters takes place on gameto-genesis, leading to the formation of new zygotic types. Until F_3 is reached it is impossible to say which of these are homo- and which hetero-zygous. It is therefore still uncertain to what extent the coloured types in F_2 owe their colour to the creation of coloured gametes in cases where both pure types were white.

[Note added December, 1904.

Sowings from the F_2 plants, produced by E. H., long × E. H., round, showed that at least 8 types of purple F_2 plants exist, each type having a different F_3. Some purples breed true, proving that there is a real gametic synthesis of purple. The P. L. plants of F_2 can give no purples, but may breed true. The picotees may give whites, or tinged whites, or may breed true, but give no purples or P. L. Tinged whites may breed true, or may give whites only, in addition. All whites, creams, and round-pollened F_2 plants, of course, breed true to those characters. At least four types of colour-gametes may be formed by F_1.

The Black Knights (deep chocolate-purple), which occurred as new forms in F_2 from Firefly (red) × E. H., long, have also bred true.]

9. After the break-up of the parental characters in F_1 from white × colour the re-constitution of the gametes may evidently proceed on different plans in the various cases, but the number of whites (more strictly plants with uncoloured cell-sap), averages about 1 in 4—the total being 570 white, 1846 coloured, or 1 : 3·24.

The coloured parent in the cases examined was almost entirely broken up, and only reappeared occasionally in F_2.

10. When both parents are white and F_1 is coloured, the evidence shows that after total reversion to purple the half-reversion forms appear in F_2; but when F_1 is a half-reversion the converse does not occur. Gametes bearing colour are formed in the first and probably

in the second case also. The number and characters of these are as yet unknown, but it is clear that great fluctuations occur.

11. The "Cupid" (dwarf procumbent), and the "Snapdragon" shape of flower are ordinary Mendelian recessives to the normal.

POULTRY.

(Experiments made by W. Bateson and R. C. Punnett.)

The following table shows the results obtained respecting comb characters and extra toes. The numbers prefixed to the experiments enable the reader to trace the relationships in the case of all cross-bred birds. To save space the relationships of the pure-bred birds are not given. No case was seen in which this was found to influence the result. Slight and equivocal indications of a change of "prepotency" due to in-breeding were mentioned in Report I. Fuller experience strongly suggests that these appearances were due to accidental fluctuations.

In the tables, DR is F_1, $\frac{DR}{2}$, $\frac{DD}{2}$, are, respectively, heterozygous and homozygous dominants in F_2.

$\frac{R}{2}$ is extracted recessive in F_2.

The asterisk (*) means that the bird had some special origin, which can be ascertained from the breeding. R*, for instance, may mean R from DR × R, or R appearing in F_1 (see Report I, p. 116), etc. These distinctions must be indicated, but they do not seem to affect the results.

p.p., r.r., mean that the bird was proved to be pure pea or pure rose; i.r., i.p. and p.s., that it was proved to contain single.

Doub. means the longitudinally *split single*, described later.

r.p. is the rose-pea, or "walnut" comb, whether natural (Malay) or artificial.

The same bird is given as DD in its matings with a single, and as r.r. or p.p., in its matings with one of the dominants.

1902.

Pen.	Exp. No.	♀.	Origin (numbers refer to expts.).	Cb.	Ft.	Used in exp.	♂.	Origin (numbers refer to expts.).	Cb.	Ft.	Used in exp.	Combs. Nature of mating.	Combs. Offspring. r.	r.p.	p.	s.	Dubious.	Feet. Nature of mating.	Feet. Offspring. e.	½ e.	No e.
1	89	27	5	p.			new Br. L.		s.			DR × R			7	15					
	90	91	5	p.			,,		,,			,,			12	21					
	91	540	73	s.	e.		,,		,,			R* × R				22		DR × R	10		14
2	92	523	77	,,	,,		W. L.		,,			,,				59		,,	26		34
3	93	122	Dor.	r.	,,	26	59	I. G.	p.			r.r. × p.p.		5				D × R	5		
4	94	664	I. G.	p.		152 and 186	531	Dor.	r.	e.	151 and 152	p. × r.r.		18				R × D	20	2	
	95	586	Br. L.	s.		151 and 176	,,	,,	,,	,,		R × D	45					,,	45		2
	96	47	W. L.	,,			,,	,,	,,	,,		,,	33					,,	34		1
	97	547	,,	,,			,,	,,	,,	,,		,,	28					,,	28	2	
5	98	483	,,	,,		165 and 193	579	36	p.			$R \times \frac{DR}{2}$			13	21					
	98*a*	384	I. G.	p.			,,	,,	,,			? p.p. × p s.			8						
6	99	472	40	s.			464	85	s.	no e.		$\frac{R}{2} \times \frac{R}{2}$				38		$R \times \frac{(DR)}{2}$	18		20
	100	530	38	r.	no e.	179 and 121	,,	,,	,,	,,		$\frac{DR}{2} \times \frac{R}{2}$	11			9		,,	11		10

	101	565	W. L.	s.		167	,,	,,	,,	,,		$R \times \frac{R}{2}$				52	,,	30		29
	102	493	85	r.	,,	178	,,	,,	,,	,,		$\frac{DR}{2} \times \frac{R}{2}$	8			5	$\frac{R}{2} \times \frac{(DR)}{2}$	1	1	10
8	103	440	38	,,	e.	157	435	82	s.			$\frac{DD}{2} \times R^*$	36				$\frac{DR}{2} \times R$	25		16
	104	317	70	s.	,,		,,	,,	,,			$R^* \times R^*$				22	$DR \times R$	7		13
9	105	4 ♀ s.	74	,,	,,		608	65	,,			$R^* \times R^*$	4 doubs.			131	,,	58	8	68
10	106	416	I. G.	p.		68	419	I. G.	p.		64 to 67	i.p. × i.p.			2	1				
	107	378	W. L.	s.		77, 158, and 117	,,	,,	,,			R × i.p.			9	5				
	108	372	,,	,,		122	,,	,,	,,			,,			7	4				
	109	114	,,	,,			,,	,,	,,			,,			9	11				
	110	644	I. G.	p.			,,	,,	,,			DD × i.p.			25		[644 was (W. L. × I. G.) × I. G.]			
	111	262	Dor.	r.	e.	78	,,	,,	,,			i.r. × i.p.	5	2	3	2	$D \times R$	11	1	
11	112	607	25	,,	,,		558	W. L.	s.		145 to 147	$DR \times R$	23			16	$DR \times R$	15		24
	113	511	85	,,	,,		,,	,,	,,			$\frac{DD}{2} \times R$	36				$\frac{DR}{2} \times R$	24		13
	113*a*	85	24	,,	,,		,,	,,	,,			$DR \times R$	19			15	$DR \times R$	16		20
	114	534	25	,,	,,		,,	,,	,,			,,	25			30	,,	19	1	36
12	115	453	85	,,	no e.		G. Dor.		s.	e.	158 to 161	$\frac{DR}{2} \times R$	21			24	$\frac{R}{2} \times D$	41	3	2
	116	520	85	s.	e.		,,		,,	,,		$\frac{R}{2} \times R$				34	$\frac{DR}{2}$? × D	29		3
	117	378	W. L.	,,		77, 158, and 107	,,		,,	,,		$R \times R$				37	$R \times D$	37		3
	118	590	72	r.	e.	159	,,		,,	,,		$DR \times R$	12			18	? × D	31		

1902—*continued.*

Pen.	Exp. No.	♀.	Origin (numbers refer to expts.).	Cb.	Ft.	Used in exp.	♂.	Origin (numbers refer to expts.).	Cb.	Ft.	Used in exp.	Combs. Nature of mating.	Combs. Offspring. r.	r.p.	p.	s.	Dubious.	Feet. Nature of mating.	Feet. Offspring. e.	½ e.	No e.
14	119	450	85	s.	e.		560	38	s.	e.		$\frac{R}{2} \times \frac{R}{2}$				20		$\frac{DR}{2} \times \frac{DR}{2}$	12	1	8
	120	452	85	,,	,,	155	,,	,,	,,	,,		,,				14		,,	11		3
17	121	530	38	r.	no e.	100 and 179	544	,,	r.	no e.		$\frac{DR}{2} \times \frac{DD}{2}$	26					$\frac{R}{2} \times \frac{R}{2}$			- 27
	122	372	W. L.	s.		108	,,	,,	,,	,,		$R \times \frac{DD}{2}$	39					$R \times \frac{R}{2}$			45
	123	683	51	p.			,,	,,	,,	,,		$p.s. \times \frac{r.r.}{2}$		36				,,			44
	123*a*	514	85	r.	e.		,,	,,	,,	,,		? × RR	6					$?\frac{DD}{2} \times \frac{R}{2}$	7		
18	124	{ 61 63 }	29	,,	,,	37	667	22*a*	p.			r.s. × p.s.		68		24		DR × R	43	4	48
	125	4 ♀ s.	17	p.		34	,,	,,	,,			DR × DR			43	16	2				
19	126	546	W. L.	s.		174	471	I. G.	,,		178 to 180	R × D			37						
	127	463	,,	,,		143	,,	,,	,,			,,			42						
	128	529	I. G.	p.		153	,,	,,	,,			i.p. × p.p.			6						

20	129	573	38	s.	,,	181	552	38	s.	e.		$\frac{R}{2} \times \frac{R}{2}$			43	$\frac{DR}{2} \times \frac{DR}{2}$	39		8
	130	151	58	p.		81	,,	,,	,,	,,		$DR \times \frac{R}{2}$		42	42	$R \times \frac{DR}{2}$	44		41
21	131	508	86	s.	no e.	146	488	86	,,	min. e.	183	$R^* \times R^*$			36	$\frac{R^*}{2} \times \frac{DR^*}{2}$	12	3	21
	132	631	77	,,	c.		,,	,,	,,	,,		,,			56	$DR \times \frac{DR^*}{2}$	41	1	21
	133	532	86	,,	,,		,,	,,	,,	,,		,,			41	$\frac{DR}{2} \times \frac{DR^*}{2}$	32	3	9
23	134	234	16	p.			461	85	r.	no e.	184 to 187	$p.s. \times \frac{r.r.}{2}$	33			$R \times \frac{(DR)}{2}$	17	1	17
	135	609	19	,,		160 and 185	,,	,,	,,	,,		,,	8			,,	6		5
	136	527	W. L.	s.		184	,,	,,	,,	,,		$R \times \frac{DD}{2}$	21			,,	10		13
	137	47	15	p.			,,	,,	,,	,,		$p.s. \times \frac{r.r.}{2}$	12			,,	7		4
24	138	2 ♀ s.	51	s.			608	65	s.			$R^* \times R^*$			36				
25	139	3 ♀ s.	75	,,	,,	192	638	75	r.	e.	192	$R^* \times DR$	60		46	$DR \times DR$	76	5	32
27	140	47	W. L.	,,			651	63	p.			$R \times DR$		4	5				
	141	547	,,	,,			,,	,,	,,			,		6	3				
28	142	2 ♀ s.	Egyp. doub.				Eg. ♂	doub.						28 *doub.*					

1903.

Pen.	Exp. No.	♀.	Origin (numbers refer to expts.).	Cb.	Ft.	Used in exp.	♂.	Origin (numbers refer to expts.).	Cb.	Ft.	Used in exp.	Combs. Nature of mating.	Combs. Offspring. r.	r.p.	p.	s.	Dubious.	Feet. Nature of mating.	Feet. Offspring. e.	½ e.	No e.
1	143	463	W. L.	s.		127 and 191	Eg.		doub.	no e.			37	split							
	144	4 ♀ s.	Eg.	doub.	e.		,,		,,	,,			35	,,						Mixed	
2	145	876	124	p.	e.		558	W. L.	s.		112 to 114	$\frac{DR^*}{2} \times R$			10	12		$DR^* \times R$	13		9
	146	508	86	s.	no e.	131	,,	,,	,,			$R^* \times R$				27		$R^* \times R$			29
	147	983	103	r.	e.		,,	,,	,,			$DR^* \times R$	9			16		$DR' \times R$	14		11
3	148	79	111	p.	,,			Andal.	,,			,,			4	5		$DR \times R$	4		5
	149	498	40	s.				,,	,,			$\frac{R}{2} \times R$				25					
	150	16	Mal.	r.p.				,,	,,			r.p. × s.		5	3						
4	151	586	Br. L.	s.		95 and 176	531	W. Dor.	r.	e.	94 to 97	$R \times D$	18					$R \times D$	19		
	152	664	I. G.	p.		94 and 186	,,	,,	,,	,,		p. × r.r.	? 1	16				,,	16	1	
	153	529	,,	,,		128	,,	,,	,,	,,		i.p. × r.r.	1	1							
5	154	939	90	s.			915	90	p.			$R^* \times DR$			30	36					
	155	452	85	,,	,,	120	,,	,,	,,			$\frac{R}{2} \times DR$			8	7	1	$\frac{DR}{2} \times R$	8	1	8

6	156	969 833 906	134 ,, 137	r.	,,		984	134	r.	,,		$\frac{?\,DR^*}{2} \times \frac{DR^*}{2}$	51			24		$DR^* \times DR^*$	40	1	35
	157	440	38	,,	,,	103	,,	,,	,,	,,		$\frac{DD}{2} \times \frac{DR^*}{2}$	5					$\frac{DR}{2} \times DR^*$	3		2
11	157a	4♀ s.	115–116	s.	,,		766	115	s.	,,		$R^* \times R^*$				63		*Mixed*	[54	2	7]
12	158	378	W. L.	,,		77, 107, and 191	G. Dor.		,,	,,	115 to 118	R × R				10		R × D	10		
	159	590	72	r.	,,	118	,,		,,	,,		DR × R	6			4		? × D	10		
	160	609	19	p.		135 and 185	,,		,,	,,		,,			3	3	1	R × D	7		
	161	17	Mal.	r.p.			,,		,,	,,		r.p. × s.		9	10			,,	18		
13	162	881	137	,,	,,	172	904	93	r.p.	,,		r.p. × r.p.		4				DR × DR	2		2
	163	9	new W. L.	s.			,,	,,	,,	,,		s. × r.p.	10	14	13	6		R × DR	14		31
	164	956	Br. L.	,,			,,	,,	,,	,,		,,	11	12	8	16		,,	13	1	33
	165	483	W. L.	,,		98 and 193	,,	,,	,,	,,		,,	17	20	16	16		,,	30	4	35
	166	548	,,	,,			,,	,,	,,	,,		,,	5†	5	1	8		,,	7		11
	166a	710	,,	,,			,,	,,	,,	,,		,,	1	0	1	1		,,	2		1
15	167	565	,,	,,		101	842	124	,,	,,		,,	16	16	14	11		,,	34		23
	168	Br. L.		,,			,,	,,	,,	,,		,,	2	5	4	12	1	,,	7	2	14
	169	Buff. Legh.		,,			,,	,,	,,	,,		,,	7	7	6	8		,,	12	1	14
	170	Blk-red Game		,,			,,	,,	,,	,,		,,	7	7	8	6		,,	14		14
	171	16	Mal.	r.p.			,,	,,	,,	,,		r.p. × r.p.	1	3	1	1		,,	5		1
	172	881 887	137 135	,,	e.	162	,,	,,	,,	,,		,,	16	53	22	12		$DR^* \times DR$	73	8	20
17	173	844	124	,,	no e.		855	137	,,	no e.		,,	1	14	4	0		$R^* \times R^*$			19
	174	546	W. L.	s.		126	,,	,,	,,	,,		s. × r.p.	22	18	15	21		$R \times R^*$			75

† Includes 1 *double* r.c.

1903—*continued.*

													Combs. Offspring.						Feet. Offspring.		
Pen.	Exp no.	♀.	Origin (numbers refer to expts.).	Cb.	Ft.	Used in exp.	♂.	Origin (numbers refer to expts.).	Cb.	Ft.	Used in exp.	Nature of mating.	r.	r.p.	p.	s.	Dubious.	Nature of mating.	e.	½ e.	No e.
	175	985	134	r.p.	no e.		855	137	r.p.	no e.		r.p. × r.p.	9	24	12	4		R* × R*			47
	176	586	Br. L.	s.		95 and 151	,,	,,	,,	,,		s. × r.p.	6	14	9	11		R × R*			40
	176*a*	3	,,	s.			,,	,,	,,	,,		,,	21	11	10	17	1 doub.	,,			60
	176*b*	853	W. L.	s.			,,	,,	,,	,,		,,	17	10	7	8		,,			42
18	177	760 849	105	doub.	e. no e.	195 194	799	Br. L.	s.			doub. × s.	50 *doub.*			20		Mixed	[15	3	52]
19	178	493	85	r.	no e.	102	471	I. G.	p.		126 to 128	r.s. × p.p.		12	16			$\frac{R}{2} \times R$			28
	179	530	38	,,	,,	100 and 121	,,	,,	,,			,,		21	14			,,			35
	180	777	100	,,	,,		,,	,,	,,			,,		50	41			$\frac{R^*}{3} \times R$			92
20	181	573	38	s.	e.	129	867	105	doub.	,,		s. × doub.	9 *doub.*			23		$\frac{DR}{2} \times R$	12		17
	182	849	105	doub.	no e.		,,	,,	,,	,,		,,	27	,,		30		R* × R			57
21	183	938	90	s.			488	86	s.	min. e.	131 to 133	R* × R*				34		$R \times \frac{DR^*}{2}$	18		18

23	184	527	W. L.	,,		136	461	85	r.	no e.	134 to 137	$R \times \frac{DD}{2}$	9					$R \times \frac{(DR)}{2}$	4	1	5
	185	609	19	p.		135 and 160	,,	,,	,,	,,		$p.s. \times \frac{r.r.}{2}$	10	13			1	,,	7		16
	186	664	1. G.	,,		94 and 152	,,	,,	,,	,,		$p.p. \times \frac{r.r.}{2}$		10				,,	4		6
	187	649	63	p.			,,	,,	,,	,,		$p.s. \times \frac{r.r.}{2}$	10	17				,,	10		16
24	188	8	new W. L.	s.			Mal.		r.p.			s. × rp.	1	4	3	2		?	0	2	8
	189	Buff.	Legh.	,,			,,		,,			,,	6	7	8	8					
	190	796	90	,,			,,		,,			,,	10	8	8	9					
	191	378 463	W. L.	,,		77, 107, and 127	,,		,,			,,	4	3	1	1					
25	192	3 ♀ s.	75	,,	c.	139	638	75	r.	c.	139	R* × DR	100			110		DR × DR	133	8	72
27	193	483	W. L.	,,		98 and 165	866	105	doub.	no e.		s. × doub.		3 *doub.*		5		R × R*			8
	194	849	105	doub.	no e.	177	,,	,,	,,	,,		doub. × doub.	30	,,		16		R* × R*			47
	195	760	105	,,	e.	177	,,	,,	,,	,,		,,	19	,,		10		DR* × R*	8	2	19

DISCUSSION OF RESULTS.

I. *Comb-characters.*

DR birds, r. or p., produced in various ways, bred with R birds (s.c.) of various origins gave 449 D to 469 R. DR × DR gave a total of 211 D to 83 R. These totals* are not very far from the 1 D : 1 R or 3 D : 1 R severally expected. Individually, however, there are some wide departures from these expectations, and it is practically certain that in several cases there was distinct numerical inequality of D and R gametes, as seen in the case of Peas and elsewhere. On the other hand there is no indication that DR individuals themselves are capable of subdivision into classes, and all the figures available point to a monomorphic distribution of the aberrant individuals round the mean case of equality in output of D and R. There is also distinct evidence that the proportional output of D and R may change at different times in the life of the same individual. There is, as yet, no clear case, unfortunately, in which a DR ♂ giving an aberrant number with one s.c. ♀ was simultaneously bred with another s.c. ♀. It is practically certain, nevertheless, that the irregularity did not, in any way, depend on the recessives, for the same bird often gave regular numbers with 1 DR and aberrant numbers with another. In these comments it is assumed that no gametic selection occurs.

"Extraction" had no influence on the proportions, as may be seen from the table.

An example of a ♀ extracted pure dominant (rose) occurs in	Experiment	103 and 157
Another, ditto	,,	113
An example of a ♂ extracted pure dominant (rose) occurs in	,,	121—123A
Another, ditto	,,	134—137
Another, ditto	,,	184—187

Very few F_2 p.c. birds have been tested, and, as it happens, no case of pure extracted dominant F_2 has been met with, but ♀ 644 from DR × D was, however, a pure DD (Experiment 110).

Purity of Recessive (*Single*) *Comb.*—Singles of various origins, derived in several ways from rose and from pea crosses, when mated together, have never given either rose or pea. In all, such matings have given 800 singles. In one case (Experiment 105) *four specimens of a new form of comb* appeared, together with 131 singles (included in total just given).

This mating was made of 4 F_1 recessive ♀'s from a "non-Mendelian" or mixed F_1 from rose-comb, bred with a similar F_1 recessive ♂ from pea-comb. In the four mutational birds the combs were imperfectly split posteriorly (see p. 113). These must be regarded as illustrations of that twinning or duplicity which has been observed in so many median organs. A similar case of posterior duplicity in a rose-comb* came in Experiment 166. Such double "single" combs are not very rare in fowls, but are not found in any recognised breed, the Houdan "leaf" comb being, in some ways, distinct.

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* They include chicks kindly bred by Mr. Assheton (not given in the table) from birds raised in Experiment 33, as follows: DR × R, 16 r. 6 s. DR × DR, 36 r., 16 s.

Relation of Rose to Pea Comb.—In 1902 this inquiry was begun by crossing DR rose-combs with DR pea-combs (Experiment 124). These birds may respectively be called r.s. and p.s. They gave, as was expected, four types of comb, viz., s.s. singles, r.s. roses, p.s. peas, and finally r.p. combs, the latter being a type not before seen in the course of the work.† It is characteristic of their comb that it is wide like a rose, though much less papillose and with no posterior point or "pike"; but the most singular feature of it is the *presence of small bristles or minute feathers on the posterior third.* Often these feathers form a narrow band crossing the comb from side to side in front of the posterior third. Sometimes, however, there is no definite band, but the feathers are either generally distributed over the back or on the posterior sides of the comb. No such bristles or feathers ever occur on singles, roses, or peas. Their existence raises a morphological problem of some interest, but this cannot be treated as yet. In front of the feathered part of the comb is often a well-marked transverse groove. On approaching maturity the part anterior to the groove generally widens out (especially in males) and becomes corrugated, the posterior part remaining narrow and flat.

This peculiar comb is the structure known as the "walnut" comb, proper to Malays and to no other breed of fowls. As stated, it was here first formed indirectly by crossing r.s. × p.s. and it has since been made directly by breeding both pure r. and extracted F_2 r.r. with pure p. Sometimes it is distinctly larger than in pure Malays, but the artificial walnut comb is often indistinguishable from the pure Malay type.

The results from the "artificial" walnut combs were as follows. Three such r.p. ♂'s were bred through the season of 1903 with various s.c. birds (Experiments 163—170, 174, 176, 176A—B), and gave—

	r.p	r.	p.	s.
	139	142	112	141 + 2 doubtful.
Simple expectation ...	*133*	*133*	*133*	*133*

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* In 1904 a case of partial duplicity in a pea-comb has occurred. A split s.c. like the mutational form occurred also in Experiment 176A.

† The features of the 3 forms of dominant were not satisfactorily distinguished in the earlier chicks from Experiment 124. They are therefore given collectively as 68 r., rp., p. and 24 s.

Four "artificial" r.p. ♀'s with similar ♂'s gave (Experiments 162, 172 and 173, 175)—

	r.p.	r.	p.	s.
	95	26	38	16
Simple expectation	*99*	*33*	*33*	*11*

We have, therefore, in the first case a fair approach to equality, and in the second, figures not very far removed from 9 : 3 : 3 : 1. It is, therefore, clear that the artificial r.p. birds were giving off approximately equal numbers of gametes, r.p., r., p., s. The individual results show some irregularities, especially 176B, which gave 10, 17, 7, 8, but the average result is unmistakable.

These facts show two points of interest, first, that some gametes are bearing r.p. *unsegregated;* secondly, that s. is evidently present though it is presumed that in the parental gametes of the r.s. and p.s. birds the s. elements had been eliminated by segregation.

At first sight it seemed that the presence of s. indicated a failure of segregation. Further experiment, however, has shown that r.p. birds raised from *pure* r. and *pure* p. birds are in exactly the same condition as those raised from r.s. × p.s. This latter observation, which will be described with the work of 1904, proves that s. gametes may in some way be formed by resolution of the product of the cross r. × p.

The next step was to investigate the properties of the true Malay walnut, or natural r.p. comb, and especially to determine whether it could be resolved into r. and p. Mr. Edgar Branford, of Woodbridge, who has a long experience of the breed, was kind enough to give much help in this matter, and further assistance was also received from Mr. Wootten, a breeder of White Malays. It appears that Malays bred *inter se* sometimes produce true peas as well as the normal walnut. Occasionally in certain strains peas come often, but generally speaking they are uncommon. Whether pure Malays ever throw actual roses or singles is not quite certain, but if they do, these occurrences must be excessively rare.

A pure black-red Malay ♂ and two pullets were obtained from Mr. Branford. The ♂ had been used by him in 1902 with pure hens, and certainly then gave no rose or single, though possibly occasional peas.

The Malay ♂ was bred with 5 s.c. hens of various origins and gave (Experiments 188–191).

r.p.	r.	p.	s.
22	21	20	20

the equality of the four types of gamete being evident. The Malay hens are notoriously bad layers and only gave small totals. Each was bred with a s.c. cock and the result was

r.p.	p.
14	13, no true r.c. or s.c.

Of the pea-combs, 3 were of the high, intermediate type, inclining to s.c., but none was a true s.c. Of the r.p. group, 1 on hatching was regarded as an irregular rose, but it developed into a fairly ordinary type of walnut comb, though having two rather prominent knobs behind.

In Experiment 171 a Malay ♀ is recorded as giving × artificial r.p. ♂, 3 r.p., 1 r, 1 p., 1 s. The r. was irregular, and the s. was very low. In the light of later experience, it is perhaps possible that both were wrongly classified. Both were dead in the shell, and at that date the distinctions were not familiar to us.

In these results there are still certain points obscure. The "artificial" r.p. birds are giving off the four types of gamete. Therefore there must be five types of r.p. comb possible, namely r. × p., r.p. × r.p., r.p. × r., r.p. × p., r.p. × s.; but owing to the fact stated above, that s. may be created afresh by at least one of the combinations into which it does not directly enter, the subsequent analysis becomes very complex.

A further difficulty is suggested by the behaviour of the natural r.p. Though the ♂ r.p. with s. ♀'s gave the four forms in equal numbers, it is practically certain that in Malay breeding, if r.c. and s.c. are ever seen, they are excessive rarities; whereas if there were gametic equality on both sides, 3 in 16 should be r.c., and 1 in 16 should be s.c. For some time the conclusion seemed irresistible that the appearance of these forms on crossing with s. must be due to some imperfection of fertilisation, leading to a partial monolepsis,* and this account was provisionally adopted. At that time the difference between reciprocal crosses was not fully appreciated; but after a critical study of their material it is more likely that the true explanation lies in a difference of constitution between the ♂'s and ♀'s.

It is possible that only ♂'s with walnut combs produce all four kinds of gamete, r.p., r., p., s., other males giving only r.p., or r.p. and p., or r.p. and r.; while r.p. ♀'s give either r.p. and p., or r.p. only. If this conclusion is substantiated, it will be possible to give a complete account of this curious case.

[Note added December, 1904.

Extensive inquiry among Malay breeders has now made it practically certain that real rose or single combs do not occur among Malays when bred pure. The problem created by their absence must still be regarded as unsolved.

We have examined the combs of a great number of Malays in the best strains of the West of England. The males evidently present two fairly distinct types: (1) Saddle-shaped, more or less papillose in front; (2) a narrower comb, in which the "working" is in the form of corrugations. Probably it is only the former (1) which gives off rose; but as such birds are freely used for breeding, the entire absence of rose-combed chicks cannot be attributed to selection of males of type (2) exclusively.

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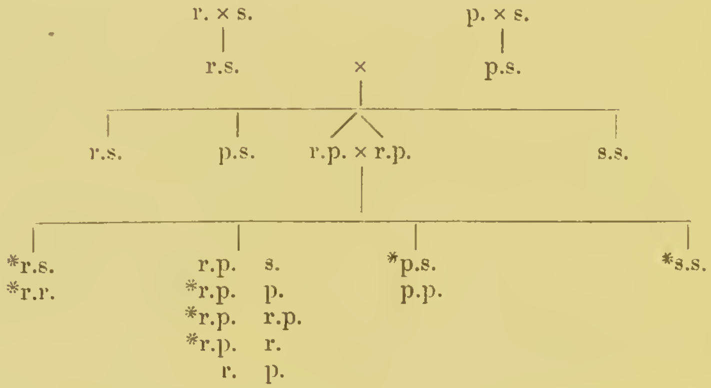
* See Report I, p. 155.

The work of 1904 has shown that 2 ordinary r.p. Malay ♂'s were r.p., p., and a Malay Bantam ♂ was r.p., r. Two ordinary r.p. Malay ♀'s proved to be r.p., r.p., and one proved to be r.p. p. One such ♀, however, is recorded as having given (× s.c. ♂), 1 r.c., and 2 s.c. chicks, besides 1 p.c. and 1 r.p. On the hypothesis suggested in the text, this should be impossible. Unfortunately there is an element of uncertainty in these particular records, and until this ♀ has been tested again the question must be left undecided. Two Malay Bantam ♀'s proved to be r.p. r.p.]

Experiment 156 proves that r. birds derived from r.s. and p.s. carry only r. (or r. and s.), p. having been excluded. The work of 1904 similarly has proved that s. from s. × r.p., whether natural or artificial, is also pure; and that r. or p. from combinations of any r.p. × s. are similarly free from p. or from r. respectively.

Finally, by the mating of two r.p. birds (bred from r.s. × p.s.), at least one homozygous r.p. has been produced, proving that here an actual synthesis of r. with p. has been effected. The facts may be set out thus



The asterisk (*) marks the combinations already met with experimentally.

Mixed F_1 from $R \times S$ and $P \times S$.

The meaning of these mixtures was discussed in Report I, p. 116, and the applicability of two hypotheses was considered. The further course of the inquiry has all tended to disprove the second hypothesis, which supposed a failure of dominance in the R birds of F_1. Such birds and their posterity have behaved as pure R, except for the production of the four split-comb birds in Experiment 105.

Further evidence on this question is provided by Experiments 126–7, in which 471 ♂ was proved pure p. though he came from 17 ♀ × Gr. ♂ which *both* gave mixed F_1 (Experiments 49–51 and 46–8). Therefore, whatever the "impure" character may be, a pure dominant may be segregrated from it.

Next there is the important result seen in Experiment 111. Dork. ♀, 262, was raised from "impure" parents K ♀ × K ♂ (Report I, p. 114). She was proved "impure" in Experiment 78, and in Experiment 111 by I. G., 419 ♂ (proved "impure" in Experiments 64–7 and 107–9), she gave 5 r., 2 r.p., 3 p., 2 s. Singles are thus produced from impure rose × impure pea, though each of these can have had no s.c. ancestor for an indefinite number of generations.

Taken in connection with the fact that s.c. gametes may be formed by F_1 from pure r. × pure p., it is difficult to resist the conclusion that an impure r. or p. is really a bird in the condition of one of de Vries' "*Halb-rassen*" and is giving off an unknown proportion of a second gamete, here s.c. Such a conclusion harmonizes well with the fact given in Report I, p. 116, *Note*, that a pure strain of r.c. occasionally throws a s.c. bird, and that when fresh blood is introduced, the proportion of s.c.'s greatly increases. These facts have perhaps a bearing on the behaviour of the Malay r.p. just described, but the exact relation of the two sets of phenomena is not yet clear.

The attempt to increase the proportion of s.c. in mixed F_1 by inbreeding the s.c. parent has failed in the case of White Legh., owing to the strain becoming delicate and dying out. The Br. Legh. strain, though persistently inbred, has developed no such delicacy, but no result of the kind has been witnessed in the case of combs (all the Br. L. birds in the Tables not marked "new" belong to the inbred strain). In the case of the foot-character it is just possible that there is a positive effect of this nature.

SPLIT S.C.

The behaviour of these mutational forms has been imperfectly studied, and thus far is quite anomalous (see Experiments 181, 182, 193 to 195). In 182 we have split × split giving approximate equality, 27 split to 30 s., but the same split ♀ × another split ♂ gave 30 split to 16 s.c. It is probable that the dominance of the split comb is very irregular. To investigate the behaviour of an established split comb we received through the great kindness of Mr. Stanley Flower, specimens of split-combed fowls from Cairo, mentioned in the writings of Mr. F. Finn. The fowls were common bazaar birds and have presumably not been selectively mated. The comb is not unlike that of our own splits, but the separation was greatest *posteriorly* instead of anteriorly. This proved to be a distinct dominant over s.c. and nothing novel has yet been obtained respecting it. The experiments are being continued to test certain questions as to cresting and will be given in detail hereafter.

II. *Extra Toes.*

As was described in Rep. I (Experiment 88 and pp. 119 and 129), the normal foot, though commonly recessive, may sometimes *dominate* over the extra-toe character, and this heterozygote may give equality when bred with recessives, just as if it were an ordinary DR. The investigation of subsequent generations, therefore, becomes very complex, though the gametic segregation of the characters can be demonstrated with fair certainty. Having these difficulties in view, the experiments were arranged primarily with regard to the more amenable problems of the combs, the feet being studied only incidentally.

From the fact that the no-e.t. character may dominate, we must expect that on an average the departures from simple Mendelian expectation will be in the direction of excess of no-e.t. birds, and this is the case, various forms of DR × R giving in all

	Both e.	1 e.	no e.
1902	399	18	456
1903	240	12	307
	639	30	763

Adding the 30 cases of 1 e.t., there were, therefore, only 669 e.t. birds to 763 no e.t. Similarly, various forms of DR × DR gave in all 412 e.t., 27 halves, 212 no e.t.; the cases of 2 or 1 e.t. together give only 439 to 212 no e.t., or 2·07 : 1.

There can be no doubt that the excess of recessives is due to the occasional dominance of the no e.t. character.

One ♂, 544, and one ♀, 530, without e.t., from Experiment 38 (unmixed F_1 group), and one ♀, 493, from Experiment 85 (mixed F_1 group) were proved to be pure recessives in that character. A similar ♀ (from ♀ 493 × no-e.t. ♂ 464, which was proved to be heterozygous in that character) was similarly proved to be pure. Collectively, these recessives gave 271 birds without trace of e.t. (Experiments 121 to 123, 178 to 180). The ♀, 508, from Experiment 86 was similarly a pure recessive (Experiments 146 and 131).

In addition to ♂ 305 (Rep. I, p. 118), two other birds (464, 461) without e.t. have proved themselves to be ordinary heterozygotes in respect of foot-character (Experiments 99 to 102, 134 to 137, 184 to 187). In one case also a ♂, 488, which had, on hatching, been counted as no e.t., was afterwards found to have each hallux slightly thickened, with a *minute extra nail* pressed to the normal on one foot. This bird also behaved like an ordinary DR (Experiments 131 to 133).

In the case of the ♂, 461, just mentioned, the output of e.t. and no-e.t. gametes (or conceivably the dominance) differed greatly in the 2 years. In 1902, with various no-e.t. ♀'s, he gave (Experiments 134 to 137) 40 e.t., 1 half, 39 no e.t., but in 1903 (Experiments 184 to 187) he gave 25 e.t., 1 half, 43 no e.t., a striking excess of recessives. Similar changes at different periods have been seen in other cases, though less pronounced.

We are led to the conclusion that if an individual be heterozygous, there is no direct relation between the somatic character it presents and the gametic output. Nevertheless, it would be expected that since a no-e.t. "DR" shows dominance of that character, similar aberration of dominance might appear in its offspring. Thus far, however, only a slight indication of such a result has been found. Taking, for instance, the various cases of DR × R, the totals from the mixed F_1 group gave 335 e.t. or 1 e.t., to 339 no e.t.; and from the unmixed F_1 group 334 e.t. or 1 e.t., to 364 no e.t. The difference of about 10 per cent. may well be due to this cause, but it is scarcely emphatic enough to make the point clear in view of the fact that the departures from equality occurred in both groups in both directions without any striking disparity.

Amongst the various forms of mating indicated by DR × R, the cases were distributed as follows:—

	e.t.	½ e.	no e.
(1) DR × R	336	21	439
(2) $\frac{(DR)}{2} \times R$.........	125	3	151
(3) $\frac{DR}{2} \times R$	113	1	95
(4) R × DR*.........	18	—	18
(5) $\frac{R^*}{2} \times \frac{DR^*}{2}$	12	3	21
(6) DR* × R*	35	2	39
	639	30	763

Here DR is the ordinary F_1. $\frac{(DR)}{2}$ indicates F_2 birds with no e.t., but heterozygous. $\frac{DR}{2}$ is the heterozygous e.t. form in F_2. DR* a dominant heterozygote otherwise produced (see tables). R the pure-bred no e.t. R* a pure no e.t., otherwise produced.

There is an obvious suggestion that the different results in (2) and (3) may be due to the dominance of the no e.t. in (2), but the general run of the results is too irregular to warrant much confidence on the point, especially in view of the equality (77, 1, 78) given in Experiment 88 by an F_1 no-e.t. bird. Similarly, the material is too heterogeneous to indicate the average ratio of dominant no-e.t. gametes to recessive no e.t., though, presumably, there is an underlying regularity here also.

Among dominants in F_2, 3 ♂'s and 6 ♀'s proved to be DR and none DD,* but of these only 3 ♀'s had the toes sufficiently well-marked to be possible DD, having been selected for comb characters. One or more ♀'s in Experiment 157A (from DR × D) were presumably DD, but they were not separately tested.

It should be noticed that the Silver-grey Dorking ♂ in Pen 12, 1902, though of the purest strain attainable, threw 8 no e.t. in 149 chicks. In 1903, however, the same ♂ gave 45 chicks, all e.t. (for hens see table). From our experience and from such information as has been received from breeders, an occasional no-e.t. chick is given off from time to time by the purest strains, and must be regarded as comparable with the "*semi-latent*" characters of de Vries.† It need scarcely be said that no parent without full-sized extra toes can have been used in such a strain for an indefinite number of generations.

An anomalous case also occurred (Experiment 188) in which a Wh. Legh. ♀ × Malay ♂ gave 2 chicks (out of 10), having 1 e.t. each. The ♀ was given to me by Mr. Lister-Kay, and belonged to his famous strain. It seems likely that this must be regarded as an original variation.

Slight feathering on the shanks has also from time to time been seen in birds from the Dorking crosses, but this has not been followed up.

III. *Colour.*

The colour phenomena are in several respects complex, though the general behaviour is fairly simple. As stated in Rep. I, F_2 from white (Leghorn or Dorking) × brown (Ind. Game or Br. Legh.) consists of about 3 light : 1 dark. The *light* class is made up of pure white birds, white birds with "ticks" (barred or plain), and from Br. Legh. × Wh. Dork.—some pile, viz., yellow or chestnut and white. No true pile has yet come from Ind. Game and White, though ♂'s in F_2 (and F_1) often have red or yellow splashes as well as dark ticks.

The *dark* class consists of brown birds, somewhat like the parent, cuckoos, and blacks. Each kind may have an irregular amount of white. Three ♀'s (F_2 from Br. Legh. × Wh. Dork.) have appeared of the brown type, *spangled* more or less regularly with white, having the coloration of Spangled Old English Game. From the same mating also a few true Silver-grey or Duckwing hens came in F_2, but hitherto no ♂.

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* Unless 514 (Experiment 123A) be such a bird, she gave only 7 chicks, all e.t.

† (Mut., I, p. 424; compare case of s.c. from r.c., p. 113).

Some, at least, of these F_2 types must be regarded as resolved forms. Their properties are being gradually worked out, and for the present a detailed account is deferred.

The following points have been made out since the last Report :—

The unticked birds are sometimes in great excess over the ticked.

The ratio of light to dark is very constantly about 3 : 1, the present totals (1903), counting pile as light, being 537 : 173, or, adding Experiment 130, p. 103, 603 : 187. DR × white gives, with great constancy, about 1 : 1, the totals being 210 light : 215 dark.

A pure white F_2 ♀ × similar ♂ gave (Experiment 131) 36 light without ticks; and with a pure white ♂ (Experiment 146) she gave 27 without ticks.

One (if not both) of the F_2 whites was, therefore, pure DD in white.

All dark birds in F_2 bred together, or with other dark birds, gave exclusively dark birds.

Two Silver-grey hens, mentioned above, were bred with a pure Duckwing or Silver-grey Dorking, no such ♂ having come in F_2. They gave (F_3) 78 Silver-grey chicks. Of these, again, 4 ♀'s, bred with own brother, gave, in 1903, 63 Silver-grey chicks. Most of these were typical Silver-greys, but a few had white splashes or were a little light in colour. The original F_2 Silver-greys must, therefore, have been, as anticipated, homozygous in respect of that colour.*

There can be little doubt that the spangled type is similarly homozygous.

Dominance of White and Exceptional Cases.

Among the many hundreds bred from a pure white parent with coloured or DR birds, only two are recorded as having come dark. Of these, one was probably due to a mistake in marking the egg. The second *may* have been referable to the same cause, but there is no definite reason for doubt in this case. For the present, both cases should be counted as exceptions.

The subsequent breeding has proved that each of the 3 Cr., White Dorking birds (Rep. I, p. 93), were impure in whiteness, being in all probability DR of white over some colour.† The K. White Dorkings, however, were pure.

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* In F_4 one pied bird, White and Silver-grey, has occurred. Whether such birds ever come in pure Silver-grey strains we do not know.

In F_2, from Brown Leghorn × White Leghorn, two Silver-greys have now come, proving therefore that such birds in Brown Legh. × Wh. Dorking are not simply attributable to Grey Dorking ancestry in the case of White Dorking.

† Later experiments have shown that a pure race of *white with minute ticks*, usually one or two, when crossed with colour gives *dark* F_1. Hence the Cr. birds probably were heterozygotes of white × ticked white. February, 1905.

As regards the Cr. birds, the proof was as follows:—

Cr. 121 ♀ put up a buff feather in each wing on the second moult. By a Brown Leghorn ♂, she gave 4 dark, 3 with buff down (not reared), 1 pile, 10 light, 2 recorded as doubtfully light. Two of the dark and the pile were the only ones reared.

Cr. 122 ♀ was never seen to show a coloured feather. Nevertheless, by an Ind. Game ♂ (Experiment 93) she gave 2 dark, 3 light. These were the "exceptions" mentioned in Rep. I, p. 141, *Note.*

Cr. ♂ never showed a coloured feather. He was never bred with a coloured hen directly, but as stated (Rep. I, Experiment 38), six—then unexpected—dark chicks came in 102 F_2 by him out of White Leghorn ♀. These F_2 were from 3 ♀'s.

There is, therefore, no doubt that all three birds were heterozygous in colour, and the ♂ in Experiment 38 with one or more of the 3 F_1 hens was similarly heterozygous. Consequently, the darks from 122 ♀ should not have been counted as exceptional. Unfortunately, only one mating between the three Cr. birds was made, viz., 122 ♀ × Cr. ♂, producing 6 chicks. None were dark, but 2 only were reared, both white, without ticks, so far as is known.

One of the F_2 just named was used as ♂ with DR ♀ 151 (see Experiment 81), and gave (Experiment 130) 66 light, 14 dark, where the simple expectation is 60 : 20.

The conclusion from these facts is that a bird may be heterozygous though no coloured feather is to be found, and the various supposed exceptions disappear. A similar explanation, no doubt, would hold in respect of the at-first-sight anomalous result in Experiment 40.

The excess of unticked birds over ticked in F_2 from brown × white obviously points to the same conclusion.

Heterozygous Nature of Blue in Andalusians.

In the last Report (p. 131) we stated that the Andalusian colour is probably heterozygous, inasmuch as it is alleged never to breed true. By the courtesy of Mrs. Blacket Gill, one of the leading fanciers of this breed, the information was given that up to the date of inquiry in 1902, her birds had given 17 white-splashed, 36 blues, 22 blacks. Birds were subsequently obtained from her as follows: a white-splashed ♀, a black ♀, a blue ♂.

By the blue ♂ the white ♀ gave 34 blue, 20 white-splashed, and the black ♀ gave 27 blue, 19 black. In each case the result is qualitatively what would be expected if the blue is a heterozygote of black × splashed white; but whether the departure from equality indicates that some gametes bear the unsegregated blue, or may merely be taken as individual irregularities, cannot yet be stated.

The same blue cock was bred with a black hen from Experiment 40 (in which the dark birds were unexpected), F_2, from White Wyandotte × Wh. Legh., giving as offspring 10 black, 15 slaty black to bluish. Hence, therefore, it is evident that the black ♀ was a homozygous black. The 10 blacks are the result of the union of the black gametes from the Andalusian ♂ with those of the ♀, and the 15 slaty resulted from the meeting of the black of the hen with the white-splashed from the Andalusian.

NOTES ON THE PROGRESS OF MENDELIAN STUDIES.

During the 2 years that have passed since the publication of Report I the growth of Mendelian literature has been so rapid that it is impossible to give any adequate summary here. We can only specify the more significant results of recent work.

New Mendelian Cases.—The valuable memoir of Coutagne* on heredity in the silkworm, written without a knowledge of Mendel, shows that several of the characters studied have a Mendelian inheritance. Of the larval characters both black colour and transverse striping are evidently dominants to the normal whitish colour. In most of the cases white silk is dominant to yellow silk, one race presenting an exception to this rule. An artificial race of dark moths also showed a partial dominance (with some blending) over the normal light colour. This dark race was made by the use of two dark males which seem to have arisen as a sport. These were bred (1889) with the brownest females which could be found in a normal race, and from the offspring a dark race was produced by selection in about 5 years.

In the case of each of these characters the gametic segregation was evidently complete or almost complete, and the purity of the recessives at least was established in numerous experiments. Apart from cases of mixture of DR and DD, some irregularities are noticeable, but the general course of the inheritance is quite clear. Three larvæ were seen which were black on one side and white on the other, an important phenomenon occasionally seen in discontinuous variations of Lepidoptera, comparable, no doubt, with gynandromorphism.

In contrast with Mendelian inheritance of these discontinuous characters, the character, called by Coutagne, *richesse de soie* shows, to all appearances, continuous variation and a non-Mendelian inheritance, not undergoing any sharp gametic segregation, and being capable of intensification by gradual selection. It is likely that this quality depends on numerous factors.†

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* 'L'hérédité chez les Vers à Soie. Bull. Sci., Fr. and Belg.,' 1902, vol. 37.

† Coutagne's memoir contains very many facts of great importance which cannot be referred to here. The attention of students of evolution is also called to the same author's "Recherches sur le Polymorphisme des Mollusques de France," 'Soc. Agric. Sc. Ind. de Lyon, 1895,' a treatise of altogether exceptional value on the interrelations of varieties and the significance of locality.

A peculiar case of recessive variety, generally female, has been pointed out by Doncaster* in the case of *Abraxas grossulariata* var. *lacticolor* on the experimental evidence obtained by G. H. Raynor.

From the records of former experimenters there could be little doubt that the long-styled form in *Primula* is recessive to the short-styled, and experiments in progress (begun by W. Bateson in conjunction with R. P. Gregory) have confirmed this view. It is, however, doubtful as yet whether any *pure* short-styled plants exist, F_1 being a mixture of longs and shorts, of which the longs breed true. Whether the mixture is due to heterozygosis in the thrums used, or to a perpetual production of long-style gametes as a *Halb-rasse* by the short-styled plants, is not quite certain.† Horticulturists have decreed that the pin-eye is the correct form of *P. sinensis*, but all Auriculas and Polyanthuses must be thrums. Owing to the recessive nature of the long style, the short style has been totally eliminated from most English collections of *sinensis*, and now is only to be procured with difficulty. But there is apparently no *Auricula* or *Polyanthus* which breeds true to thrum eye, though such strains would certainly be in demand. Hence we are led to infer that the persistent appearance of the pin-eye is due to a perpetual output of recessive gametes by the thrums (see later paragraph on Sex, p. 128). The homostyled type which is also characterised by a great extension of the yellow centre or eye is recessive to both long and short style. For continued opportunities of studying the breeding of *P. sinensis* at Reading we are greatly indebted to Messrs. Sutton & Sons. A detailed account of these observations will be prepared later. Further observation has confirmed the statement in Report I that the fern-leaved type is recessive to the palm-leaved, segregating from it perfectly, with very rare exceptions. The green stem is similarly recessive to reddish stem, but the deep red stem is also recessive to the reddish. The curious form known as "ivy-leaved" is also a recessive to palmate leaf, segregating perfectly from it. *Double* flowers constitute a recessive character, as in Stocks (see p. 33).

As regards colour inheritance there are some complications not fully explored. Pure white on a green stem is almost certainly recessive to all colours, but the white strains on coloured stems may sometimes give white F_1, even when the other parent is a fully coloured type. On this point the evidence is not altogether consistent, and more inquiry is needed. It is possible that the presence or absence of colour in the stem affects the result.

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* 'Ent. Rec.,' 1903, vol. 15, p. 142.

† From the later evidence there is little doubt that pure short-styled plants exist. February, 1905.

Blue may be almost entirely broken up on crossing, rarely reappearing in F_2, probably as 1 in 16.

The case of certain pink-flaked and mauve-flaked types is of more practical importance. The pink is recessive and breeds true at once. The mauves, on the other hand, may throw pinks. Savings from individual plants showed that some are pure or DD mauves and others are heterozygotes of mauve and pink. A pure strain of mauves may be immediately obtained by saving from a homozygous mauve.

The work of Biffen has greatly extended the application of Mendelian principles in the case of wheat (see 'Jour. Agric. Sci.,' I).

Castle* has found the rough, "rosetted" or "Abyssian" condition of the coat in guinea-pigs dominant over the normal smooth coat, and that the Angora coat is recessive to the normal in both rabbits and guinea-pigs.

We are indebted to Mrs. Staples-Browne, of Bampton, for a game Bantam cock and two hens bred from ♀ brown-red × ♂ black-red, both believed to be pure. All three are very near the brown-red in colour. The two hens have the purple or "gipsy" face of the brown-red, almost, if not quite as well developed as pure brown-reds. The cock's face, though showing a tinge of purple, is more nearly the ordinary red. This dominance of so novel a character as brown-red and purple face is somewhat exceptional. In their down the F_1 chicks are said to have been very dark, thus also resembling the brown breasted.

The paper just published by A. Lang contains evidence, which as the author states, goes far to show that the well-known discontinuity between the banded and bandless *Helix hortensis* depends on Mendelian segregation.† The bandless character is dominant.

The poultry cases here related illustrate the simultaneous segregation of *four* allelomorphic comb-characters.

Biffen (*loc. cit.*) has found *primâ facie* evidence for the belief that in wheat, power of resisting rust is a recessive character. The remarkable case referred to by Orton‡ in cotton seems rather to indicate that resistance to the wilt disease is a dominant character.

Reversion.—When F_1 presents a character distinct from that of either parent, it is not rarely reversionary. In addition to the cases hitherto noticed, an interesting one was exhibited by Hurst at the Southport Meeting of the British Association, white Angora rabbit × Belgian hare giving F_1 grey like a wild rabbit. These experiments are in progress and will be published hereafter.

The cases given above respecting Sweet Peas are of a somewhat distinct type, as in them two entirely white or "albino" plants gave a coloured reversion, which in some families was complete, to the wild purple type, and in other families took the form of "half-reversion" to the red bicolour "Painted Lady" type. This is a well-known and ancient type of the cultivated flower, said to occur wild in Sicily.

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* 'Science,' N.S., vol. 18, 1903.

† 'Festsch. z. Siebzigsten Geburtstage v. E. Haeckel,' 1904, pp. 482, 503.

‡ 'U.S. Dep. of Agric. Bull.,' No. 27, 1900.

The appearance of hoary F_1 as the result of crossing certain glabrous Stocks is one of the few examples of reversion in a "structural" character as distinguished from colour (see later, p. 124).

Special interest attaches to the behaviour of yellow flowers in their crosses. It is to be remembered that yellow may be due to various physiological types of pigmentation, and the evidence is complicated by the frequent occurrence of reversion in F_1. Cream Stocks and white for instance, give purple F_1. Cream Sweet Peas may do the same. Correns* found that in *Mirabilis jalapa* yellow and white always gives red. The evidence from generations of Sweet Peas and Stocks later than F_2 plainly shows that there may also be simple dominance of *white*, viz., no *coloured* plastids, over cream, or coloured plastids. Correns states that in his *Mirabilis* F_1 there was no trace of yellow (except a spot in a mosaic). Mr. Lynch has called our attention to the case of *Begonia Weltonensis* (pink), from *B. Sutherlandi* (orange), and *B. Dregei* (white), which is perhaps comparable. Before the relations of these dissimilar illustrations can be compared, the nature of the yellow in each case must be determined. In the Begonia case it is not impossible that the pink of the hybrid is due to dominance of the sap-colour from *Sutherlandi* while its chromoplastic yellow is recessive.

Monolepsis.—In considering this subject (Report I, p. 155), we were not aware that a suggestion very similar to our own had been proposed by Giard.† Further information respecting Orchid cases was given by Hurst.‡ In connection with Millardet's original observation on the Strawberry, a record of Andrew Knight§ respecting a case in the Strawberry, possibly of a similar nature, is interesting. Further information as to the phenomenon is greatly to be desired, and it is unfortunate that the recorded cases relate to subjects, which for various reasons are difficult to experiment with.

Mixture of forms in F_1.—In certain cases two types which each breed true separately, give, on crossing, individuals of two or more kinds. If this complication is not determined by sexual dimorphism, one or other of the two pure types must, in reality, be giving off more than one type of gamete. There are then two possibilities only. Either the difference between these types of gamete lies in the characters with which they are endowed in gameto-genesis, or in the manner in which they are affected by fertilisation. In the former case we must conceive of the gametes of the parental type A being, in reality, *xA* and *yA* ; in the latter they may be called *xyA*, but on fertilisation with some other pure type there is a partial monolepsis, by which on fertilisation with B, sometimes the result is xAB, and sometimes *yAB*, and not always *xyAB*. Up to the present time there is no case which can be positively declared to be of the latter class, but as monolepsis certainly occurs in the complete form, the possibility of partial monolepsis should not be forgotten. For a long time it seemed that the phenomena seen in Malay crosses must point to this interpretation, but further experience is not favourable to that suggestion.

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* 'Ber. Deut. Bot. Ges.,' vol. 20, 1903, p. 605.

† See especially Giard, 'C.R. Soc. Biol.,' 1903, vol. 55, p. 779, and 'Cinquantenaire Soc. Biol.,' p. 12.

‡ 'Gard. Chron.,' 1903, ii, p. 227.

§ 'Trans. Hort. Soc.,' vol. 5, 1824, p. 294.

In most of the recorded instances of mixed F_1 there is now no doubt that the first is the true account. In discussing the results of Crampe attention was called* to the possibility that the dissimilarity between two F_1 forms from "pure" parents might turn on a hidden distinction *either* between the different albinos, *or* between the different coloured parents, and that in certain cases of Parsons the distinction was certainly in the albinos, most giving pied offspring while self-coloured F_1 came from others.

At this point the recent paper of Cuénot† marks a very important advance. Mixed F_1 has been several times recorded in mice, some families containing blacks and greys, though the parents in each case seemed to be pure. It had appeared to us that here the probable interpretation lay in impurity of the coloured parents, but Cuénot has now proved that albinos extracted from the several colours will give those colours on crossing with coloured types.

Still more significant is his proof that by crossing albinos of different extraction the allelomorphs determining the various colours *will themselves segregate* in the gametogenesis of the albino in ordinary Mendelian fashion. For example, albino *ex* yellow bred with albino *ex* black gives a heterozygous albino whose gametes are in equal numbers bearers of the factors which determine to black or to yellow respectively. When such an albino breeds with a pure colour-type, a mixed F_1 may result. As he points out, this fact disposes of various outstanding difficulties met with by Darbishire and others. The appearance of the two reversion types in Sweet Pea is almost certainly determined by similar factors, though the proof can only appear next season.

[Note added December, 1904.

Tschermak‡ had previously brought forward a large mass of facts of a similar nature, and (in view of Cuénot's evidence) his account is clearly correct, applying perhaps to all cases where F_2 gives the ratio 9 : 3 : 3 + 1. It is, however, doubtful whether we should speak of such factors as "latent." It is rather that an element is present which when it meets another element produces a certain character in the fertilised result. This is not the character which was latent. As stated later, there is still a case, that of hoariness resulting from the crossing of glabrous Stocks, to which no adaptation of this simple view is yet applicable.]

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* W. Bateson, 'P.Z.S.,' 1903, ii, pp. 78 and 84.

† Cuénot, 'Arch. Zool. exp. et gén., Notes et Rev.,' 1904, vol. 11, pp. 45 to 56.

‡ 'Beihefte zum Bot. Cbltt.,' vol. 16, 1903, Heft. 1.

Peculiarities of Extracted Types.—In addition to the fact observed by Cuénot that an extracted type (*e.g.*, albino) may carry on segregable determinants, whereby the individuals may, in reality, differ from each other, though outwardly alike, there are other specific properties of extracted types which call for notice. At an early stage in the inquiry it was remarked that though gametic unions between certain pure types give reversion, unions between extracted gametes, ostensibly similar to the pure ones, give no reversion. This has now been seen most clearly in Sweet Peas where, so far, two dissimilar recessives (long white × round white) of the same extraction, crossed together, give no reversion, though the plants used are indistinguishable from the two original types which gave the reversion. Moreover, in Stocks when one such extracted is crossed with one of the *original* pure types, there is no reversion, though a *new* pure type may cause the reversion again. Conversely, in Stocks, $DR_1 \times DR_2$, where D is a white hoary, may give some glabrous, while $DR_1 \times DR_3$ give only hoary.

These phenomena must be distinguished from that described by Cuénot; for in the cases now under consideration the quality which determines or prevents the reversion is apparently common to all the sister cross-breds and does not depend on any segregable or allelomorphic character. Therefore, though the process, so far as we yet know is quite specific in its results, it is not Mendelian. In view of these facts the nature of the reversionary forms in F_2 is often problematical. The relation of the two phenomena is a question which only the later generations can solve.

With the facts just described, may be compared the results obtained in Stocks, where among the glabrous types, not only white × red, and cream × red give reversion to hoary, but the same reversion occurs when white is crossed with cream. Therefore, the reversion cannot be regarded as merely due to the meeting of a pair of elements, of which one is borne by each type, but it must have some more complex causation.

Resolution and Disintegration: Synthesis.—The conception of resolution applies properly only to those cases where a character appearing in F_2 is constituted by the breaking up of the compound allelomorphs of the original parents, the term disintegration being reserved for cases when the integrity of an allelomorph is impaired and segregation is incomplete. Thus the occurrence of homozygous types in F_2 made as a blending or mosaic of the original parental allelomorphs is an indication of disintegration. For instance, the white-spangled types seen in F_2 from Brown Leghorn × white, and certain chequered types, similarly produced, must be regarded as acquiring their colour from the coloured parent, and their white from the white parent, which is then disintegrated.

In view of Cuénot's evidence great care will be needed in discriminating these various cases. The uniformity of F_1 will generally be a guide to the nature of the case, but at least the homozygous nature of the F_2 type in question must be tested in each instance. It is not inconceivable that, owing to dominance and other peculiarities of heterozygosis, F_1 may be uniform though the gametes of one or other parent are not so, and a spurious appearance of resolution may thus appear in F_2. In such cases sensible uniformity in the statistical composition of F_2, together with proof of homozygosis of resolved forms, will furnish the only reliable criterion as to real resolution in F_1.

It should be especially noted that the phenomenon detected by Cuénot, while simplifying some cases, formerly interpreted as resolution, does not provide a substitute for that conception; for, to go no further, we still have to deal with cases where one of the original pure types practically disappears from F_2, etc., having evidently been entirely or almost entirely broken up in the gametogenesis of F_1 (*e.g.*, blue flower-colour in *Primula sinensis*, the red of some sweet peas, pp. 121 and 90).

As to the statistical relations of the products of resolution there is, as yet, no evidence which is quite satisfactory, and it is clear that several types of cases occur. The case of *Antirrhinum* studied by de Vries* seems to be peculiar in the fact that, on crossing red × white only 1 white in 16 appeared in F_2.†

An intensification of one of the pure parental characters is not rare in some members of F_2 where resolution occurs. Perhaps the most striking illustration is that seen by Biffen (*loc. cit.*, p. 31) in the case of lax ear in Wheat. A similar case in colour is given, p. 90.

Tschermak's‡ cases of resolution in *Matthiola* are, thus far, the most fully studied, F_3 having been already reached. They give valuable indications as to the statistical relations in a case where resolution follows on reversion in F_1; though, for this reason, the precise interpretation of the phenomena is somewhat obscure.

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* 'Mutationstheorie,' vol. 2. p. 198.

† [*Note added December*, 1904.—In 'Camb. Phil. Soc. Proc.,' vol. 12, p. 50, I suggested that this result might be attained if F_1 produced 4 types of gametes in equal numbers. Mr. R. H. Lock has pointed out to me that the case may very probably be regarded as an *actual* example of "di-hybridism." If this proves to be true there is then no resolution or synthesis to be reckoned with, and the original red would not be, gametically, a compound character.—W. B.]

‡ 'Beihefte z. Bot. Cbltt.,' 1903, vol. 16, p. 18.

All the available facts support the expectation that a symmetry will be found to prevail in the distribution of the resolved characters comparable with that occurring in the case of unresolved characters in ordinary mono-hybrids.

It is desirable that the term synthesis should be restricted in heredity to the permanent union of component allelomorphs to form a compound allelomorph which breeds true without segregation. Such an example is seen in the case of the "walnut" (r.p.) comb, produced by crossing rose-comb with pea-comb. The F_1 comb, thus artificially formed, may be scarcely, if at all distinguishable from the natural "walnut" comb of the Malay breed. F_1 produces four types of gametes (probably in equal numbers), r.p., r., p., s. Among the F_2 types there are, therefore, some birds formed by r.p. × r.p., and the evidence (1904) proves that some, at least, of these are then really synthetic r.p., breeding true to that character.

Tschermak's discovery that after the production of reversionary purple F_1 in *Matthiola*, certain purples appear in F_2 which seem capable of breeding true, probably points to a similar permanent synthesis.* Here, however, a complex resolution has evidently taken place, and possibly these cases may prove to be analogous with the production of various homozygotes after resolution; for the degree to which the compound allelomorphs of the new forms derive elements from both pure types is not yet determined.

Heterozygous Breeds.—As an illustration of a breed permanently heterozygous, the Andalusian fowl was given tentatively in Rep. I. Experiments have now shown that this is the true account. The blue Andalusian gives off gametes, black and white-splashed. The blue is formed by heterozygosis of these two, but the black and the white-splashed birds, produced by mating blues together, are homozygous and generally breed true. Further study of the Giant Lavender, *Primula sinensis*,† has confirmed the view that this also is a heterozygote of magenta and white-tinged, offering an exact parallel to the Andalusian. In each case there is, however, a doubt as to whether the white-splashed or tinged may not, in certain cases, subsequently segregate into a purer white and a form more distinctly coloured, possibilities which require further investigation.

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* [*Note added December*, 1904.—Our later results with Sweet Peas prove that there also a synthesis has occurred, forming purple-bearing gametes, and bicolour-bearing gametes. A strain of pure purple and of pure bicolours can thus be produced from F_2 made by white × white. The same is true for the picotee and tinged white types in F_2.

Darbishire's results ('Biometrika,' vol. 3, Part 1, pp. 24, 25) are without doubt capable of a similar explanation. Some of the greys in F_2 and later generations are evidently in composition grey × grey or some other colour. The deficiency of albinos in the matings where such greys were used is therefore in harmony with the facts seen in Sweet Peas, Stocks, etc., as must appear at once when the offspring of each individual are made separately traceable in the Tables.]

† W. Bateson, 'Mendel's Principles of Heredity,' 1902, p. 182.

Sex.—In Report I we indicated the possibility that sex may be ultimately a phenomenon of gametic segregation comparable with that seen in ordinary Mendelian cases. In an interesting essay, Castle* has greatly amplified this suggestion, and has shown reasons for believing that the segregation of male spermatozoon from female spermatozoon and of male ovum from female ovum may occur at the reduction-division in gametogenesis. While admitting the likelihood of this suggestion, we feel that for the present it should be received with caution. In particular, we doubt the conclusion that *both* ova and spermatozoa (after a reduction-division) are always bearers of either the male or the female character. It seems more likely that special cases will present special phenomena in this respect. As yet the evidence most applicable to the decision of the question is thus derived from those reciprocal crosses which give dissimilar results, and in view of the idiosyncrasies of these cases, we incline to expect that sometimes the male element, sometimes the female, will be found to be responsible for sexual differentiation, and that the similar differentiation of both elements is not likely to be universal. For instance, if the case of Malays, already discussed (p. 111), be shown to bear the suggested interpretation, it is evident that the gametes of one sex alone, probably the male, and not both, will determine the sex of the offspring. One sex must then be regarded as a "Halbrasse" of the other, just as long style may, perhaps, be of short style in Primula.

The evidence of Correns† as to Bryony crosses has a direct bearing on this question. Using *Bryonia alba* ♀ as seed-plant and *B. dioica* as male, he obtained offspring all diœcious (with a doubtful exception). As he states, this fact points to the segregation of the sex-determinants among the male cells of *Bryonia.* The result of the reciprocal cross will be awaited with interest.

Gärtner,‡ however, using ♀ *Lychnis diurna* × ♂ *L. flos cuculi* (♀) also obtained F_1 all diœcious, males and females, pointing to sex-segregation among the egg-cells of the mother. In each of these cases, unfortunately, the problem is complicated by the appearance of sterility in F_1, and in the case of ♀ *L. diurna* × ♂ *Silene noctiflora* (♀) the results were somewhat ambiguous.§

A case that may be used for the elucidation of this problem is that of the Cinnamon Canary, recently described by Norduijn,* who has most kindly given us much supplementary information. As to the essential facts, Canary-breeders seem to be agreed. The Canary has two forms which are both in a sense albinos, the yellow and the cinnamon. The latter, in the nestling stage at least, has red eyes, which subsequently darken, but red eyes may occur also in yellows. When green (viz., non-albino) ♀'s are crossed with cinnamon ♂'s, both greens and cinnamons are produced, of which the males are always and the females sometimes green, but *the cinnamons are invariably female.* From the reciprocal cross the young are always green.

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* 'Bull. Harvard Mus.,' vol. 40, 1903.

† 'Ber. Deut. Bot. Ges.,' 1903, vol. 21, p. 195.

‡ 'Bastarderzeugung,' p. 49.

§ *Ibid.*, p. 287.

The F_1 males from cinnamon ♂, when bred with green or yellow ♀'s, may again produce cinnamons which are exclusively ♀. The interpretation of this case is still quite obscure, but attention is called to it as a most important subject of experiment. The facts strongly suggest that there is here some phenomenon of gametic coupling† of the female sex-character with cinnamon. When yellows are used the results are complicated by the appearance of reversionary heterozygotes, green or green-marked.

Castle is doubtless right in the view that marked inequalities observed in the distribution of characters between the sexes after crossing are due to some similar coupling of a sex-character with some allelomorphs,‡ and the investigation of these cases will probably much elucidate the real nature of sexual differentiation. The phenomenon of sex is possibly comparable in some aspects with that of the "*Mittelrassen*" of de Vries, the production of one form being, in gametogenesis, constantly accompanied by the production of a second.

In the sweet-peas with sterile anthers we have a phenomenon which may be described by a slight stretch of language as Mendelian segregation of a female from a hermaphrodite (see p. 91).

Disturbances, due to sex, have been met with by several observers, a particularly striking one being recorded by Hurst (p. 148).

The Moment of Segregation.—The balance of evidence is in favour of the belief that gametic segregation takes place at the reduction-division, but no crucial test is yet forthcoming. The new evidence as to the individuality of the chromosomes and the discovery that a true transverse division occurs in the chromosomes of plants at reduction are clearly favourable to the hypothesis that the reduction-division is the critical moment. A fact which rather suggests that segregation occurs at some earlier dichotomy, is the irregularity of the individual F_2 ratios (*cf.* pp. 88 and 108) in certain cases (*e.g.*, Poultry), which strongly contrast with the extreme regularity of these ratios in the case of wheat, for example (Biffen), or maize (Lock).

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* 'Album der Natuur,' 1903, p. 71. See also Blakiston, Swaysland, and Wiener, 'The Canary Book,' Jerome, 'Canary Breeding,' 1896, etc.

† In Report I, we took exception to Correns' use of the term "conjugation" to denote this association of characters, preferring the word "correlation" already in use. Experience, however, has shown that, owing to the special uses of correlation now prevalent, the term here leads to confusion. No such objection attaches to the words "coupling" or "coupled," also introduced by Correns in the same sense, which in future we propose to adopt.

‡ For a case of a curious distribution of such varieties in a wild form, see the case of the beetle, *Gonioctena variabilis*, W. Bateson, 'P.Z.S.,' 1895, p. 850.

Up to the present time the attempt to discover an order in the occurrence of the gametes, bearing either of a pair of allelomorphs, has led to negative results. The case of *Pisum* seemed not unpromising for this inquiry, but a considerable number of pollinations of DR plants with R pollen has, so far, failed to show that the D and R ovules are arranged in any definite pattern or order, but as conceivably more than one plant* may have to be taken into account, the recognition of the arrangement may be a very difficult matter.

As to the factors which determine the retention or exclusion of any character in the case of any germ-cell, no suggestion has yet been made. It is not impossible that this may be influenced by some factor easily disturbed by environmental influences, so far, at least, as the egg-cell is concerned. To take a crude illustration, if gravitation effected the result, the regularity of the order might be obliterated by the action of the wind at the moment of segregation. Improbable as this particular suggestion obviously is, it is, perhaps, to some irregularity of a similar nature that the want of a visible order may be due.

The relation of *gametic* differentiation to the normal differentiation between *somatic* parts of the same body is one which, sooner or later, will call for consideration. There are besides many examples of differentiation between somatic organs manifesting itself in bud-sports, where the differentiating pair of characters are such as we elsewhere know to be an allelomorphic pair.

Statistical Consequences of Mendelian Heredity.—This subject has been discussed by Yule† and by Pearson.‡ In Rep. I, p. 158, we suggested "that Galton's law may be a representation of particular groups of cases which are, in fact, Mendelian," in the sense that the gametes are pure. The analysis carried out by Yule points to a similar conclusion, if the phenomena of dominance and special consequences of heterozygosis are neglected. Pearson's conclusion that various phenomena of inheritance studied by him are incompatible with Mendelian expectation is open to the objection that many of his characters are obviously liable to such great disturbances from the interference of conditions that the operations of heredity alone must be largely obliterated. In other classes of cases to which he refers (various colour phenomena) no sufficient analysis is yet provided, and in such a field comprehensive statistics are an inadequate indication as to the underlying physiological processes.

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* For example, there is every likelihood that the seeds from the right and left carpellary edges are antidromic, though all stigmas turn to the flower's right (see Macloskie, 'Am. Nat.,' November, 1895).

† 'New Phytologist,' 1902, vol. 1.

‡ 'Phil. Trans.,' 1904, 203 A, p. 53, and 'Roy. Soc. Proc.,' 1904, vol. 73, p. 262.

The experiments of Johannsen* have made an important contribution to this part of the inquiry. Taking self-fertilised beans (*Phaseolus*) he found indications that the number of "pure lines" in respect of seed-weight was very considerable. Hence we may suppose with some confidence that segregation, in respect of this character, deals with units which, though small, have a sensible size. It is to be hoped that others will be attracted to this fruitful method of research.

General.—As the results of experiments now in progress here and elsewhere will soon clear up many doubtful points, we propose to defer a general survey of the subject. Certain conclusions of significance are, nevertheless, obvious.

The solution of the various problems of heredity is now seen to depend primarily on a study of the process of segregation in gametogenesis, and secondarily on a determination of the specific consequences of the union of gametes of the various types in fertilisation. These questions can be answered only by a minute experimental analysis, and little advance can be expected from study of the phenomena in the mass by comprehensive statistical methods, however appropriate such treatment may have seemed in the absence of any knowledge of the physiological processes which constitute heredity.

In a large and rapidly increasing number of cases, it is known that segregation of characters is sensibly complete, the characters being thus allelomorphic and the gametes bearing them pure. Such allelomorphism may apparently subsist in the case of any character of animals or plants. Though naturally the phenomenon is more easily demonstrated for some characters than others, any one who conducts breeding experiments can perceive frequent indications of the prevalence of segregation in numberless dissimilar characters.

In fowls, for instance, there is no reasonable doubt that such features as late or early feathering, shortness of wing-quills and tail, peculiar qualities of voice, forms of constitutional weakness, follow rules closely similar to those detected in features more amenable to critical study. There is no reason to suppose that physiological distinctions, such as liability to disease (*cf.* p. 121, and Biffen, *loc. cit.* p. 40), late and early ripening (Biffen, p. 34), certain forms of sterility (see p. 91), and so forth, will be exempt from the operation of these rules. There are already indications, moreover, that such features may be gametically coupled with others more easy to deal with, for example, certain types of pigmentation.

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* 'Erblichkeit in Populationen,' Jena, 1903.

On the other hand, it has been asserted that certain experiments have demonstrated that gametic purity does not occur in cases where its presence might be expected, *e.g.*, the colours of mice.* It appears to us, however, that the analysis of these cases is as yet materially imperfect. The evidence in the case of *Matthiola*, for instance, shows that many complexities have to be considered before such negative propositions can be established.

Especially in dealing with extracted types caution is needed. Difference between the behaviour of an extracted and an originally pure type may evidently be caused by the presence of various determining characters, which though imperceptible until a cross is made, may modify the result. Nevertheless, these hidden characters may themselves be allelomorphic to each other in a simple Mendelian fashion (Cuénot), and the phenomena may illustrate gametic purity in the strictest sense.

Irregularities resulting from the direct action of conditions may also obscure the simplicity of the result, and mistakes of interpretation may easily occur through want of attention to this fact (*cf.* Peas, pp. 58 and 64).

EXPERIMENTS WITH POULTRY.

By Charles C. Hurst, F.L.S., Burbage, Leicestershire.

These experiments were designed in 1901, to test the Mendelian principles of heredity. Four pure breeds were selected for experimental crossing, viz., White Leghorn, Houdan, Black Hamburgh, and Buff Cochin.

Pure Breeds (P_1).

White Leghorn.—The chief characters of the breed are, clear white plumage, large single comb, four toes on each foot and yellow shanks quite free from feathers. The white plumage often acquires a yellowish tint when exposed to the sun, but the birds always moult out clear white. The down of the chick is at first yellowish white, afterwards becoming clear white. The large single comb, erect in the cock, and falling over to one side in the hen, consists of a single lobe, extending beyond the back of the head, with four to five deep and even serrations. The deep yellow shanks become lighter with age. The hens lay white eggs, as a rule, and do not sit.

Houdan.—The chief characters of the breed are, black plumage ticked or mottled with white, large crest, beard, and muffling, leaf comb, 5 toes on each foot, white shanks spotted with blue-black, usually free from feathers. This breed has an abnormal protuberance of the skull with cavernous nostrils, both of which appear to be correlated with the large crest.* The plumage is a dull blue-black shaded with brown; the white markings are irregular in size and distribution, varying from a few white ticks in the dark birds to clear white feathers in the flights and crest of the light ones. The down of the chick is clear black above with white head and underparts irregularly mottled with black. The leaf comb is an irregular structure consisting of 2 single. serrated lobes spread out somewhat like the leaves of an open book, and joined at the base by a mulberry-shaped process; it is always large in the cock and small in the hen, and varies considerably in detail in individual birds, though unmistakably different from any other kind of comb. The ideal leaf comb of the fancier has been likened to a butterfly with open wings. The extra-toe is usually a distinct digit, curving gently upwards, sometimes it is imperfect and even joined to the hallux. The pigmentation of the white shanks is variable, in some cases there are a few small spots, while in others the spots are so numerous and suffused that the shanks appear to be blue-black rather than white. The shanks are usually free from feathers, but sometimes birds appear with a few traces of feathers on the upper part of the shanks. The crest varies in size in individual birds. The hens lay white eggs and do not sit.

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* Darbishire, 'Biometrika,' vol. 3, p. 1, *passim*.

Black Hamburgh.—The chief characters of the breed are, black plumage, rose comb, 4 toes on each foot, and blue-black shanks, quite free from feathers. The black plumage has a lustrous green sheen. The down of the chick is clear black above with whitish throat and underparts, but the white disappears with maturity, leaving the bird clear black. The rose comb has a flat surface covered with a large number of small points, it is squared in front, gradually tapering backwards to a long spike or peak. The breed is small in size, close-feathered, with a neat and active carriage. The hens lay pure white eggs and do not sit.

Buff Cochin.—The chief characters of the breed are, buff plumage, small single comb, 4 toes on each foot, and yellow shanks heavily feathered down to the toes. The buff plumage varies considerably in individual birds, and also with age; the shades range from lemon to cinnamon, some of the darker cocks having quite a red tinge in their hackles and saddle feathers; black or brown feathers in the tail, white feathers in the flights, and mealy or white speckled birds are often seen in the most carefully selected strains. The down of the chick varies from light to dark buff, shaded with creamy white. The small single comb is erect in both sexes and very small in the hen. The shank-feathering varies in length and number of feathers in individual birds. The hens lay dark brown eggs, and frequently want to sit. The breed is large in size, with loose, fluffy feathers and heavy limbs.

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* *Cf.* Darwin, 'Animals and Plants,' vol. 1, p. 275, 2nd ed., 1893.

The above observations were obtained by the personal examination of more than 2000 birds of the pure breeds concerned, and in the particular strains from which the stock birds, used in these experiments, were derived.

FIRST CROSSES (F_1).

Experiment 1.—*White Leghorn* ♀ × *Houdan* ♂.

In 1902 12 White Leghorn hens were mated with a dark Houdan cockerel; eggs from this pen produced 105 chicks with the following characters:—

COMB.—*Single* ♀ × *Leaf* ♂ gave all with variable leaf combs; of these, 9 were apparently full leafs, and 96 were split leafs, having a single lobe in front split into 2 more or less concave lobes behind; there were no single combs.

DOWN.—*White* ♀ × *Black* ♂ gave 94 whites and 11 blacks; of these, 22 were apparently clear white, 72 white ticked with black, 1 black with white head, and 10 black, ticked with white. In each case the tickings were slight and inextensive, so that in the ground colour the distinction between white and black was marked and discontinuous. In the first plumage all except two of the clear whites developed black ticks, similar to those that were born ticked; the blacks developed into 6 blacks and 5 "cuckoos," 5 of the blacks were slightly ticked with white in the crest only, and in their plumage were indistinguishable from the Crève-cœur breed, the other black developed into a typical light Houdan; the 5 cuckoos were grey-white, barred with blue-black, with odd black or white feathers; both the blacks and the cuckoos were distinctly shaded with brown. Curiously enough the 6 blacks were all pullets and the 5 cuckoos all cockerels!

FEET.—*No-extra-toe* ♀ × *Extra-toe* ♂ gave 103 with e.t., and 2 with no e.t.; of these, 23 had the e.t. apparently perfect on both feet, 70 had e.t. in all stages from the almost perfect e.t. down to the mere duplication of the nail, 6 had e.t. on one foot only, while 4 had 4 toes on each foot, but in each case the hallux was elongated with extra joints, all these various states indicating digital proliferation are counted as e.t. The 2 chicks with no e.t. were apparently normal with no trace of e.t.

SHANK FEATHERING.—*Clear* ♀ × *Clear* ♂ gave 103 with clear shanks and 2 with a few traces of feathers on the upper part of the shanks; both the latter were cockerels, and one was also exceptional in having cuckoo plumage and no e.t.

SHANK COLOUR.—*Yellow* ♀ × *White* ♂ gave all with white shanks, more or less pigmented with blue-black; the cockerels without exception had very little pigment, while the pullets, with 4 exceptions, had a large amount, and at a distance appeared more blue than white in their shanks. There were no yellow shanks nor any tinged with yellow.

Egg Colour.—*White* ♀ × *White* ♂ gave all with white eggs.

Crest.—*Clear* ♀ × *Crested* ♂ gave all crested, but in every case the size of the crest, in both length and number of feathers, was reduced to about one-half.

Broodiness.—*Non-Sitting* ♀ × *Non-Sitting* ♂ gave all non-sitters.

Experiment 2.—*White Leghorn* ♀ × *Black Hamburgh* ♂.

In 1903 10 White Leghorn hens were mated with a Black Hamburgh cock; eggs from this pen produced 57 chicks with the following characters:—

Comb.—*Single* ♀ × *Rose* ♂ gave all rose combs with no trace of the single comb.

Down.—*White* ♀ × *Black* ♂ gave 49 whites and 8 blacks; of these, 1 was apparently clear white, 48 white ticked with black, and 8 black with whitish throats.

Feet.—*No-e.t.* ♀ × *No-e.t.* ♂ gave all with no trace of e.t.

Shank Feathering.—*Clear* ♀ × *Clear* ♂ gave all clear with no trace of feathers. These chicks were not reared for the observation of their mature characters.

Experiment 3.—*White Leghorn* ♀ × *Buff Cochin* ♂.

In 1903 12 White Leghorn pullets were mated with a Buff Cochin cockerel; eggs from this pen produced 60 chicks with the following characters:—

Comb.—*Single* ♀ × *single* ♂ gave all with single combs.

Down.—*White* ♀ × *Buff* ♂ gave 53 whites and 7 buffs; of these 2 were apparently clear white, 51 white patched with buff and brown, chiefly on the head, neck and breast (18 of these had also odd black ticks); the 7 buffs were all more or less patched white.

Feet.—*No-e.t.* ♀ × *No-e.t.* ♂ gave all with no trace of e.t.

Shank Feathering.—*Clear* ♀ × *Feathered* ♂ gave all with feathered shanks, but in every case the length and number of feathers was reduced to about one-half.

Experiment 4.—*Black Hamburgh* ♀ × *Houdan* ♂.

In 1903, late in the season, one Black Hamburgh hen was mated with a light Houdan cockerel, and only 6 chicks were hatched, with the following characters:—

Comb.—*Rose* ♀ × *Leaf* ♂ gave all rose combs, but they were irregular, inasmuch as the usual long peak of the pure rose was replaced by two shorter ones.

Down.—*Black* ♀ × *black* ♂ gave all blacks with white heads.

Feet.—*No-e.t.* ♀ × *E.t.* ♀ gave all with e. t. on both feet.

Shank Feathering.—*Clear* ♀ × *clear* ♂ gave all clear shanks, with no trace of feathers.

Experiment 5.—*Buff Cochin* ♀ × *Houdan* ♂.

In 1903, late in the season, one Buff Cochin hen was mated with a light Houdan cockerel, and only 5 chicks were hatched, with the following characters :—

Comb.—*Single* ♀ × *Leaf* ♂ gave all with split leaf combs.

Down.—*Buff* ♀ × *Black* ♂ gave all blacks marked and shaded with brown and ticked with white.

Feet.—*No-c.t.* ♀ × *c.t.* ♂ gave 4 with e.t. on both feet and 1 with no e.t.

Shank Feathering.—*Feathered* ♀ × *Clear* ♂ gave all with feathered shanks, but the length and number of feathers was reduced to about one-half.

Experiment 6.—*Black Hamburgh* × *Buff Cochin.*

In 1902, two Black Hamburgh pullets were mated with a Buff Cochin cockerel; eggs from this pen produced 84 chicks. At the same time one Buff Cochin pullet was mated with a Black Hamburgh cockerel; eggs from this pen produced 23 chicks. The offspring of these reversed matings had similar characters, so that all may be taken together, *i.e.*, 107, with the following characters :—

Comb.—*Rose* × *Single* gave all rose combs with no trace of single comb.

Down.—*Black* × *Buff* gave all blacks marked with brown ; of these, 82 had brown heads only, and 25 had also the body shaded with brown. In the first plumage the two sexes were quite distinct. The cockerels had golden-brown hackles, red-brown saddles, black and brown tails and wings, buff-brown breast regularly spangled with black. The pullets were as dull and sober in colour as the cockerels were brilliant, being black intermixed with light and dark brown, with darker tails and heads and spangled breasts. It seems rather curious that a cross between two breeds, each of which has normally similar plumage in both sexes, should produce offspring in which the two sexes are so distinctly differentiated.

Feet.—*No e.t.* × *No c.t.* gave all with no trace of e.t.

Shank Feathering.—*Clear* × *Feathered* gave all with feathered shanks, but in each the length and number of feathers was reduced to about one-half.

SHANK COLOUR.—*Blue* × *Yellow* gave all with light blue shanks with no trace of yellow.

CREST.—*Clear* × *Clear* gave all clear with no trace of crest.

EGG COLOUR.—*White* × *Brown* gave all with brown eggs of varied hue, none being so brown or so white as the parent breeds.

BROODINESS.—*Non-sitting* × *Sitting* gave all good sitters; all the pullets wanted to sit after laying about a dozen eggs, and all successfully hatched two lots of chicks in 1903, making excellent foster-mothers, having the strong incubating instinct of the Cochin combined with lightness of limb of the Hamburgh. The voice of the cross-bred cockerels was a ludicrous compromise between the hoarse prolonged crow of the Cochin and the shrill sharp crow of the Hamburgh. The cross-breds were intermediate in size, carriage and feathering.

In the foregoing first crosses, each of the six possible combinations of the four pure breeds has been effected, and in the one reverse cross tried (Experiment 6), no intrinsic differences could be detected in the offspring through the change of sex. Many different characters are concerned in the six matings, some are like, others are unlike. The matings of like characters in the first crosses (F_1), gave the same result as the like matings in the pure breeds (P_1). The matings of unlike characters in F_1 gave, generally, a definite dominance of one character over the other, *e.g.*, in Experiment 1, white plumage mated with black gave nearly all whites; in Mendelian terms, white was dominant over black, which was recessive. A few exceptions occurred in which the normally recessive black was apparently dominant, *e.g.*, in Experiment 1, a few were black instead of white. Among the hybrid dominants the dominance was clearly of two kinds, *complete* and *incomplete*. Complete dominance resembled the original Mendelian dominance in Peas, where no trace of the recessive character was found in the hybrid dominant, *e.g.*, in Experiment 1, a few were clear white with no trace of black. Incomplete dominance occurred when the influence of the recessive character was manifest in the hybrid dominants in varying degrees, *e.g.*, in Experiment 1, a large proportion were white ticked with black. The following table gives the total results of the first crosses (F_1), showing in (*a*) the names and numbers of the D and R characters that occurred in the unlike matings D × R, together with the respective numbers of the complete and incomplete dominants; and in (*b*) the numbers observed in the like matings R × R.

Total Results of First Crosses (F_1).

(*a*) Matings of Unlike Characters (D × R).

Expts.	Character.	D.	R.	D.	R.	Complete. D.	Incomplete. D.
1, 5,	Comb	*Leaf*	Single	110	0	9	101
2, 6	"	*Rose*	Single	164	0	164	0
4	"	*Rose*	Leaf	6	0	0	6
1, 2	Down	*White*	Black	143	19	23	120
3	"	*White*	Buff	53	7	2	51
5, 6	"	*Black*	Buff	113	0	0	113
1, 4, 5	Feet	*e.t.*	No e.t. ...	113	3	25	88
3, 5, 6	Shanks	*Feathered* ...	Clear	173	0	0	173
1	"	*White*	Yellow....	105	0	105	0
6	"	*Blue*........	Yellow....	107	0	107	0
1	Crest	*Crested*	Clear	105	0	0	105
6	Eggs	*Brown*	White	31	0	0	31
6	Broodiness ..	*Sitting*	Non-sitting	31	0	31	0
			Total ...	1254	29	466	788
			Per cent.	97·7	2·2	36·3	61·4

(*b*) Matings of Like Characters (R × R).

Expts.	R character.	D.	R.
3	Single comb	0	60
4	Black down	0	6
2, 3, 6	No e.t.	0	224
1, 2, 4	Clear shanks ...	2	166
6	No crest	0	107
1	White eggs	0	53
1	Non-sitting	0	53
	Total	2	669
	Per cent. ...	0·2	99·7

The above table shows that out of the 1283 characters observed in the D × R mating of F_1, 1254 (97·7 per cent.) were definitely dominant, the remaining 29 (2·2 per cent.) being apparently recessive. Of the 1254 dominants, 466 were apparently complete, while 788 were obviously incomplete. In Mendel's experiments with Peas, D × R in F_1 gave all complete dominants with no trace of R, but when the hybrid dominants were bred together in F_2, the R character re-appeared, proving that though not patent in F_1, it was nevertheless latent, and that the hybrid dominants raised from D × R, though apparently simple D's were in reality DR's. In these experiments with poultry it is obvious that the incomplete dominants are impure DR's, because they show the influence of the R character in F_1, in some degree, however slight it may be; but further breeding in F_2 is required to show that the complete dominants are also impure DR's, and the following experiments show clearly that such is the case.

The Mendelian expectation from the mating DR × DR in F_2 is a proportion of 3 dominants to 1 recessive. The two following experiments give the results of two such matings, in several pairs of characters, in two distinct first crosses.

FIRST CROSSES BRED TOGETHER (F_2).

Experiment 7.—*Leghorn-Houdan* ♀ × *Leghorn-Houdan* ♂.

In 1903 12 pullets bred in Experiment 1 were mated with a cockerel bred in the same experiment, and with similar characters; eggs from this pen produced 226 chicks, with the following characters:—

COMB.—DR LEAF (*single*) ♀ × DR LEAF (*single*) ♂ gave 165 leafs and 61 singles, or 2·7 D : 1 R; of these 67 were full leafs, 98 split leafs, 56 ordinary singles, and 5 singles with the hinder end somewhat thickened (*cf.* Experiment 1).

DOWN.—DR WHITE (*black*) ♀ × DR WHITE (*black*) ♂ gave 171 whites and 55 blacks, or 3·1 D : 1 R. Of these, 111 were apparently clear white, 60 white ticked with black, 32 black with white heads, and 23 black ticked with white. A few only were reared, and these developed their first plumage as in the down, except that some of the clear whites developed black ticks, and some of the blacks ticked with white developed into "cuckoos" (*cf.* Experiment 1).

FEET.—DR 5 (*4*) ♀ × DR 5 (*4*) ♂ gave 179 with e.t. and 47 with no e.t. or 3·8 D : 1 R. Of these, 167 had e.t. on both feet, 7 had e.t. on one foot only, 2 had e.t. on one foot and long hallux on the other, 1 had long hallux on both feet, 2 had six toes on each foot, and 47 had no trace of e.t. (*cf.* Experiment 1).

SHANK FEATHERING.—RR Clear ♀ × RR Clear ♂ gave 219 clear, and 7 with feather traces, or 96·9 per cent. R (*cf.* Experiment 1).

Experiment 8.—*Hamburgh-Cochin* ♀ × *Hamburgh-Cochin* ♂.

In 1903, 12 pullets bred in Experiment 6 were mated with a cockerel bred in the same experiment. Eggs from this pen produced 119 chicks, with the following characters:—

COMB.—DR ROSE (*single*) ♀ × DR ROSE (*single*) ♂ gave 89 rose combs and 30 singles, or 2·9 D : 1 R. These were respectively indistinguishable from the pure rose and single combs (*cf.* Experiment 6).

DOWN.—DR BLACK (*buff*) ♀ × DR BLACK (*buff*) ♂ gave 88 blacks and 31 buffs, or 2·8 D : 1 R. Of these, 17 were black with whitish throats, 71 black, variably marked and shaded with brown, 9 dark buff, 5 buff ticked with black, 11 light buff, and 6 creamy white. Those that were reared developed their first plumage, as follows: the blacks with whitish throats became clear black, the blacks marked with brown matured into a medley of nondescript blacks and browns, the variable buffs and creamy whites developed into buffs of various shades, some being more or less mis-marked with brown and black (*cf.* Experiment 6).

FEET.—RR 4 ♀ × RR 4 ♂ gave 119 with no e.t., or all R. Of these, 24 had malformed feet of various kinds (*e.g.*), two toes, united at the base, and bearing a single nail, otherwise they were quite healthy and vigorous (*cf.* Experiment 6).

SHANKS.—DR FEATHERED (*clear*) ♀ × DR FEATHERED (*clear*) ♂ gave 115 feathered and 4 clear, of these, approximately, 17 were fully feathered as in the Cochin grandparent, 20 three-fourths, 57 one-half, as in the parents, 13 one-fourth, 8 with feather traces on upper part of shanks, and 4 were quite clear and free from feathers (*cf.* Experiment 6).

FIRST CROSSES BRED WITH THEIR PARENTS (F_2).

The two following experiments give the results of breeding back the first crosses with one of the parents. The Mendelian expectation for the mating DR × D is all dominants: for DR × R it is equality of dominants and recessives, and for RR × R it is, of course, all recessives.

Experiment 9.—*Leghorn-Houdan* ♀ × *Leghorn* ♂.

In 1903, five pullets bred in Experiment 1 were mated with a White Leghorn cockerel; eggs from this pen produced 135 chicks, with the following characters:—

COMB.—DR LEAF (*single*) ♀ × R Single ♂ gave 74 leafs and 61 singles, or 1·2 D : 1 R. Of these, 8 were full leafs, 66 split leafs, 60 ordinary singles, and 1 single with the hinder end somewhat thickened (*cf.* Experiments 1 and 7).

DOWN.—DR WHITE (*black*) ♀ × D WHITE ♂ gave 135 whites, or all D. Of these, 66 were clear white and 69 white ticked with black (*cf.* Experiments 1 and 7).

FEET.—DR 5 (*4*) ♀ × R 4 ♂ gave 63 e.t. and 72 with no e.t., or 1 D : 1·1 R. Of these, 56 had e.t. on both feet, 4 had e.t. on one foot only, 2 had long hallux on both feet, 1 had six toes on one foot, and no e.t. on the other, and 72 had no trace of e.t. (*cf.* Experiments 1 and 7).

SHANKS.—RR clear ♀ × R clear ♂ gave 135 clear, or all R (*cf.* Experiments 1 and 7).

Experiment 10.—*Hamburgh-Cochin* ♀ × *Hamburgh* ♂.

In 1903, 12 pullets bred in Experiment 6 were mated with a Black Hamburgh cock; eggs from this pen produced 56 chicks, with the following characters:—

COMB.—DR ROSE (*single*) ♀ × D Rose ♂ gave 56 rose combs, or all D. These were indistinguishable from the pure rose comb (*cf.* Experiments 6 and 8).

DOWN.—DR BLACK (*buff*) ♀ × D Black ♂ gave 56 blacks, or all D. Of these, 34 were black with whitish throats, while 22 were slightly marked with brown, chiefly about the head (*cf.* Experiments 6 and 8).

FEET.—RR 4 ♀ × R 4 ♂ gave 56 with no e.t., or all R. All were normal (*cf.* Experiments 6 and 8).

SHANKS.—DR FEATHERED (*clear*) ♀ × R clear ♂ gave 35 feathered and 21 clear, or 1·6 D : 1 R. Of these, approximately 19, were one-half feathered as in the DR parents, 6 were one-fourth, 10 had feather traces on the upper part of the shanks, and 21 were clear and quite free from feathers as in the R parent (*cf.* Experiments 6 and 8).

So far the experiments have been confined to the same kinds of matings used by Mendel and his successors, viz: first crosses bred together (AB × AB) and first crosses bred with the parent breed (AB × A). The three following experiments are, however, rather more complicated, as in some instances three differential characters are concerned rather than the usual Mendelian pair, the matings being AB × C, AB × D, and AB × CD. In these cases it is difficult to apply the Mendelian terminology of D and R without some confusion, because some of the D's are themselves R to other D's, and some of the R's are themselves D over other R's. The omission of the Mendelian terminology in these cases may serve a useful purpose in showing that the Mendelian principles of segregation are independent of the secondary question of dominance. The three following experiments were deliberately designed to put the Mendelian principles to the severest test, and as the sequel shows, the results (though necessarily complicated) as far as segregation is concerned, agree closely with the Mendelian expectation.

FIRST CROSS BRED WITH A DISTINCT PURE BREED (F_2).

Experiment 11.—*Leghorn-Houdan* ♀ × *Black Hamburgh* ♂.

In 1903, five pullets bred in Experiment 1 were mated with a Black Hamburgh cock; eggs from this pen produced 101 chicks, with the following characters:—

COMB.—LEAF (*single*) ♀ × Rose ♂ gave 101 rose combs, or all. Of these, 58 were indistinguishable from the pure rose comb (*cf.* Experiment 2), and 43 were irregular rose combs with a double peak (*cf.* Experiment 4).

DOWN.—WHITE (*black*) ♀ × Black ♂ gave 52 whites and 49 blacks, or 1·0 : 1. Of these, 7 were clear white, 45 white ticked with black (*cf.* Experiment 2), 24 black with whitish throats, and 25 black with white heads (*cf.* Experiment 4).

FEET.—5 (*4*) ♀ × 4 ♂ gave 23 with e.t., and 78 with no e.t., or 1 : 3·3. Of these 10 had e.t. on both feet, 13 had e.t. on one foot only (*cf.* Experiment 4), and 78 had no trace of e.t. (*cf.* Experiment 2).

SHANKS.—Clear ♀ × clear ♂ gave 101 clear, or all, with no trace of feathers (*cf.* Experiments 2 and 4, 1 and 7).

Experiment 12.—*Leghorn-Houdan* ♀ × *Buff Cochin* ♂.

In 1903, five pullets bred in Experiment 1 were mated with a Buff Cochin cockerel; eggs from this pen produced 106 chicks, with the following characters:—

COMB.—LEAF (*single*) ♀ × Single ♂ gave 60 leafs and 46 singles, or 1·3 : 1. Of these, 5 were full leafs, 55 split leafs (*cf.* Experiment 5), and 46 ordinary singles (*cf.* Experiment 3).

DOWN.—WHITE (*black*) ♀ × Buff ♂ gave 52 whites and 54 blacks, or 1 : 1·0. Of these, 6 were clear white, 46 white patched with buff and brown, and some with odd black ticks also (*cf.* Experiment 3), 54 were black variably marked and shaded with brown, and some with white ticks also (*cf.* Experiment 5).

FEET.—5 (*4*) ♀ × 4 ♂ gave 45 with e.t., and 61 with no e.t., or 1 : 1·3. Of these 43 had e.t. on both feet, 2 had e.t. on one foot only (*cf.* Experiment 5), and 61 had no trace of e.t. (*cf.* Experiment 3).

SHANKS.—Clear ♀ × Feathered ♂ gave 106 feathered, or all. Of these, approximately, there were 68 half-feathered, 15 three-fourths, and 23 fully feathered (*cf.* Experiments 3 and 5).

FIRST CROSS BRED WITH A DISTINCT FIRST CROSS (F_2).

Experiment 13.—*Leghorn-Houdan* ♀ × *Hamburgh Cochin* ♂.

In 1903, 12 pullets bred in Experiment 1 were mated with a cockerel bred in Experiment 6; eggs from this pen produced 307 chicks, with the following characters:—

COMB.—LEAF (*single*) ♀ × ROSE (single) ♂ gave 139 rose combs, 77 leafs, and 91 singles. Of these; 83 were regular rose (*cf.* Experiment 2), and 56 were irregular rose combs with double peaks (*cf.* Experiment 4); 6 were full leafs, and 71 were split leafs (*cf.* Experiment 5); all the singles were normal (*cf.* Experiment 3).

DOWN.—WHITE (*black*) ♀ × BLACK (*buff*) ♂ gave 148 whites and 159 blacks, or 1 : 1·1. Of these, 20 were clear white, 87 white ticked with black (*cf.* Experiment 2), 41 white patched with buff and brown (*cf.* Experiment 3), 19 black with whitish throats, 32 black with white heads (*cf.* Experiment 4), and 108 black, variably marked and shaded brown, and some also ticked with white (*cf.* Experiment 5).

Feet.—5 (*4*) ♀ × 4 ♂ gave 127 with e.t. and 180 with no e.t., or 1 : 1·4. Of these, 108 had e.t. on both feet, 19 had e.t. on one foot only (*cf.* Experiments 4 and 5), and 180 had no trace of e.t. (*cf.* Experiments 2 and 3).

Shanks.—Clear ♀ × Feathered (*clear*) ♂ gave 195 feathered and 112 clear, or 1·7 : 1. Of these, approximately, 92 were one-half feathered, as in the male parent, 31 one-fourth, 72 had feather traces on the upper part of the shanks (*cf.* Experiments 3 and 5), and 112 were clear with no trace of feathers (*cf.* Experiments 2 and 4).

Combination of Two or Three Pairs of Characters in F_2.

So far we have dealt simply with the results of mating pairs of single characters separately, and now we have to consider how the Mendelian ratios work out when two or three pairs of single characters are taken together in individual birds. The following tables give, in black figures the Mendelian calculation of the numbers of each type expected, and in plain figures the actual numbers of each type observed in the various experiments of F_2.

The following abbreviations are used to denote the types.—wh. = white, bl. = black, bf. = buff downs; l.c. = leaf, s.c. = single, r.c. = rose combs; e.t. = extra toe, no e.t. = no extra toe on feet.

(a) *Combination of Two Characters.*

Experiment 7.

Down and Comb.

Mendelian calc.	Nos. obs.	Types.
127·1	125	wh., l.c.
42·3	47	wh., s.c.
42·3	40	bl., l.c.
14·1	14	bl., s.c.
225·8	226	

Down and Feet

Mendelian calc.	Nos. obs.	Types.
127·1	138	wh., e.t.
42·3	41	bl., e.t.
42·3	34	wh., no e.t.
14·1	13	bl., no e.t.
225·8	226	

Comb and Feet.

Mendelian calc.	Nos. obs.	Types.
127·1	135	l.c., c.t.
42·3	44	s.c., e.t.
42·3	30	l.c., no e.t.
14·1	17	s.c., no c.t.
225·8	226	

Experiment 8.

Down and Comb.

Mendelian calc.	Nos. obs.	Types.
66·9	62	bl., r.c.
22·3	26	bl., s.c.
22·3	27	bf., s.c.
7·4	4	bf., s.c.
118·9	119	

Experiment 9.

Comb and Feet.

Mendelian calc.	Nos. obs.	Types.
33·7	39	l.c., e.t.
33·7	35	l.c., no e.t.
33·7	24	s.c., e.t.
33·7	37	s.c., no e.t.
134·8	135	

Experiment 12.

Down and Comb.

Mendelian calc.	Nos. obs.	Types.
26·5	35	wh., l.c.
26·5	17	wh., s.c.
26·5	25	bl., l.c.
26·5	29	bl., s.c.
106·0	106	

Down and Feet.

Mendelian calc.	Nos. obs.	Types.
26·5	22	wh., e.t.
26·5	30	wh., no e.t.
26·5	23	bl., e.t.
26·5	31	bl., no e.t.
106·0	106	

Comb and Feet.

Mendelian calc.	Nos. obs.	Types.
26·5	27	l.c., e.t.
26·5	33	l.c., no e.t.
26·5	18	s.c., e.t.
26·5	28	s.c., no e.t.
106·0	106	

Experiment 13.

Down and Comb.

Mendelian calc.	Nos. obs.	Types.
76·7	63	wh., r.c.
76·7	76	bl., r.c.
38·3	48	wh., s.c.
38·3	43	bl., s.c.
38·3	37	wh., l.c.
38·3	40	bl., l.c.
306·6	307	

Down and Feet.

Mendelian calc.	Nos. obs.	Types.
76·7	62	wh., e.t.
76·7	86	wh., no e.t.
76·7	65	bl., e.t.
76·7	94	bl., no e.t.
306·8	307	

Comb and Feet.

Mendelian calc.	Nos. obs.	Types.
76·7	52	r.c., e.t.
76·7	87	r.c., no e.t.
38·3	41	s.c., e.t.
38·3	50	s.c., no e.t.
38·3	34	l.c., e.t.
38·3	43	l.c., no e.t.
306·6	307	

(b) *Combination of Three Characters.*

EXPERIMENT 7.

Down, Comb, and Feet.

Mendelian calc.	Nos. obs.	Types.
95·3	104	wh., l.c., e.t.
31·7	34	wh., s.c., e.t.
31·7	31	bl., l.c., e.t.
31·7	21	wh., l.c., no e.t.
10·5	13	wh., s.c., no e.t.
10·5	10	bl., s.c., e.t.
10·5	9	bl., l.c., no e.t.
3·5	4	bl., s.c., no e.t.
225·4	226	

EXPERIMENT 12.

Down, Comb, and Feet.

Mendelian calc.	Nos. obs.	Types.
13·2	11	wh. s.c., no e.t.
13·2	6	wh., s.c., e.t.
13·2	19	wh., l.c., no e.t.
13·2	16	wh., l.c., e.t.
13·2	17	bl., s.c., no e.t.
13·2	12	bl., s.c., e.t.
13·2	14	bl., l.c., no e.t.
13·2	11	bl., l.c., e.t.
105·6	106	

EXPERIMENT 13.

Down, Comb, and Feet.

Mendelian calc.	Nos. obs.	Types.
38·3	25	wh., r.c., e.t.
38·3	38	wh., r.c., no c.t.
38·3	27	bl., r.c., e.t.
38·3	49	bl., r.c., no e.t.
19·1	22	wh., s.c., e.t.
19·1	26	wh., s.c., no e.t.
19·1	19	bl., s.c., e.t.
19·1	24	bl., s.c., no e.t.
19·1	15	wh., l.c., e.t.
19·1	22	wh., l.c., no c.t.
19·1	19	bl., l.c., e.t.
19·1	21	bl., l.c., no e.t.
306·0	307	

From the above tables it will be seen that the various experiments give all the possible combination types, and that the actual numbers of these types are, on the whole, in fair agreement with the Mendelian expectation, calculated by means of the Mendelian ratios. Cases of slight deficiency or excess of certain types will, in most cases, be found to correspond with similar irregularities in the single characters. This leads to the important fact that each single character is inherited independently of the other, the combinations taking place apparently in accordance with the calculus of chance, as Mendel found in Peas. The above experiments with poultry thus confirm Bateson's previous experiments,* and show clearly that there is no correlation between the down, comb, and foot characters observed, but that each is a "unit character" with an independent inheritance.

SUMMARY OF RESULTS (F_1 and F_2).

In summarising the results of the above experiments, the most natural method will be to deal first with each character separately, *i.e.*, (1) Comb; (2) Down; (3) Feet, etc., tabulating all the results under each, in the four Mendelian expectations, viz.: (*a*) all D's, (*b*) all R's, (*c*) 3 D : 1 R, (*d*) 1 D : 1 R. The details will be briefly reviewed under each character, afterwards the grand totals of all the characters will be also tabulated in the four Mendelian expectations.

The somewhat complicated Experiments 11, 12, and 13 will be brought into line with the others by regarding their results as D's and R's simply, irrespective of their complicated matings.

(1) *Combs.*

(*a*) All D's.

Gen.	Expt.	D.	R.
F_1	1	105	0
F_1	2	57	0
F_1	4	6	0
F_1	5	5	0
F_1	6	107	0
F_2	10	56	0
F_2	11	101	0
Total observations..		437	0
Mendelian calc...		**437**	**0**

(*b*) All R's.

Gen.	Expt.	D.	R.
F_1	3	0	60
Total observations ..		0	60
Mendelian calc. ..		**0**	**60**

(*c*) 3 D : 1 R.

Gen.	Expt.	D.	R.	Ratio.
F_2	7	165	61	2·7 : 1
F_2	8	89	30	2·9 : 1
F_2	13	216	91	2·3 : 1
Total obs.....		470	182	2·5 : 1
Mendelian calc.......		**489**	**163**	**3 : 1**

(*d*) 1 D : 1 R.

Gen.	Expt.	D.	R.	Ratio.
F_2	9	74	61	1·2 : 1
F_2	12	60	46	1·3 : 1
Total obs. ..		134	107	1·2 : 1
Mendelian calc.......		**120·5**	**120·5**	**1 : 1**

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* Bateson and Saunders, Report I (1902), p. 110.

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In F_1, the Houdan leaf comb is dominant over both the Leghorn and Cochin singles (Experiments 1 and 5), in a few cases this dominance is complete and the full leaf is reproduced, while, in the majority, it is incomplete, consisting of all kinds of intermediate split leafs.

In F_1, the Hamburgh rose comb is dominant over both the Leghorn and Cochin singles (Experiments 2 and 6), and in all cases the dominance is complete, the hybrid combs being indistinguishable from the pure rose comb.

In F_1 the Hamburgh rose comb is also dominant over the Houdan leaf comb (Experiment 4), and in this we have a case of one dominant being recessive to another dominant. The dominance of rose over leaf is not so complete as that of rose over single, though more complete than that of leaf over single. No exceptions to dominance in F_1, in regard to combs, were observed in any of the experiments.*

In F_2, the hybrid dominant leafs of F_1, mated together, gave dominant leafs and recessive singles in the proportion of 2·7 : 1 (Experiment 7); mated with pure recessive singles they gave dominant leafs and recessive singles in the proportion of 1·2 : 1 (Experiments 9 and 12), and mated with dominant rose they gave all dominant rose combs (Experiment 11).

In F_2, the hybrid dominant rose combs of F_1, mated together, gave dominant rose and recessive singles in the proportion of 2·9 : 1 (Experiment 8), and mated with pure dominant rose they gave all dominant rose combs (Experiment 10).

(2) *Downs.*

(*a*) All D's.

Gen.	Expt.	D.	R.
F_1	1	94	11
F_1	2	49	8
F_1	3	53	7
F_1	5	5	0
F_1	6	107	0
F_2	9	135	0
F_2	10	56	0
Total observations..		499	26
Mendelian calc....		**525**	**0**

(*b*) All R's.

Gen.	Expt.	D.	R.
F_1	4	0	6
Total observations..		0	6
Mendelian calc. ..		**0**	**6**

(*c*) 3 D : 1 R.

Gen.	Expt.	D.	R.	Ratio.
F_2	7	171	55	3·1 : 1
F_2	8	88	31	2·8 : 1
Totals obs. ..		259	86	3·0 : 1
Mendelian calc.		**258·7**	**86·2**	**3 : 1**

(*d*) 1 D : 1 R.

Gen.	Expt.	D.	R.	Ratio.
F_2	11	52	49	1·0 : 1
F_2	12	52	54	1 : 1·0
F_2	13	148	159	1 : 1·0
Total obs. ..		252	262	1 : 1·0
Mendelian calc.		**257**	**257**	**1 : 1**

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* *Cf.* Bateson and Saunders, Report I (1902), pp. 94, 97, 98.

In F_2, the hybrid dominant leafs of F_1, mated with the hybrid dominant rose combs of F_1 gave dominant rose and leaf combs and recessive single combs in the proportion of 2·3 : 1 (Experiment 13).

Although the nature of the dominants and recessives raised in F_2 has not yet been tested in F_3, yet judging by the structural details of the incomplete dominants and the recessives of F_2 there can be little doubt that the segregation is on Mendelian lines.

In F_1 the white plumage of the Leghorn is dominant over both the Houdan and Hamburgh black (Experiments 1 and 2) and also over the Cochin buff (Experiment 3). In a few cases this dominance is complete and the clear white is reproduced, while in the majority it is incomplete, the white ground colour being ticked with black (Experiments 1 and 2) or patched with buff and brown (Experiment 3); the black ticking is slight and inextensive compared with the ground colour and the buff and brown patching is chiefly confined to the head, neck, and breast.* A few apparent exceptions to dominance of white occurred in these matings, including blacks, cuckoos, and buffs, but as the sequel shows, caution is necessary before we ascribe these exceptions to failure of dominance.

In F_1 the black plumage, both of the Houdan and the Hamburgh, is dominant over the buff of the Cochin (Experiments 5 and 6), in all cases the dominance is incomplete, the black ground colour being strongly marked and shaded with brown. The dominance of black is more complete in the down than in the adult plumage.

In F_2 the hybrid dominant whites of F_1 mated together gave dominant whites and recessive blacks in the proportion of 3·1 : 1 (Experiment 7), mated with a pure recessive black they gave dominant whites and recessive blacks in the proportion of 1·0 : 1 (Experiment 11), mated with a pure dominant white they gave all dominant whites (Experiment 9), and mated with a pure buff they gave whites and blacks in the proportion of 1 : 1·0 (Experiment 12).

In F_2 the hybrid dominant blacks of F_1 mated together gave dominant blacks and recessive buffs in the proportion of 2·8 : 1 (Experiment 8), and mated with a pure dominant black gave all dominant blacks (Experiment 10).

In F_2 the hybrid dominant whites of F_1 mated with a hybrid dominant black of F_1 gave whites and blacks in the proportion of 1 : 1·0 (Experiment 13). Although the nature of the dominants and recessives raised in F_2 has not yet been been tested in F_3, yet judging by the detailed down markings of the incomplete dominants of white and black parentage, there is little doubt that with these the segregation is on Mendelian lines, at the same time it must be pointed out that wherever the buff element is concerned in the parentage the variation is much more continuous than in F_1 (*cf.* Experiments 8, 12, and 13). It may be that white and black are elementary characters, and buff a compound one which in F_2 more than in F_1 is resolved into its component parts, or it may be that black and buff when once united in F_1 do not segregate so sharply as white and black undoubtedly do. In either case it may be significant that in F_1 the dominance of both white and black over buff is much less complete than that of white over black. Experiments are now in progress to test this question.

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* *Cf.* Bateson and Saunders, Report I (1902), pp. 95, 98.

With regard to the few apparent recessives that occurred in the white matings of F_1. I have only been able to follow up those of Experiment 1, and they have proved an interesting study. These 11 chicks were out of supposed pure white Leghorn hens by a pure recessive black Houdan cockerel (ticked with white), all were born with black down notwithstanding that their 94 birth-mates were dominant whites. These black chicks, though apparently similar in the down, developed into two distinct types in their first plumage, 6 were black and 5 were cuckoo; of the 6 blacks, 5 were practically clear black save for a few inconspicuous white ticks in the crest, these exactly resembled in their plumage the Crève-Cœur breed, the remaining black was mottled all over with white, like a typical light Houdan (this unfortunately died); the 5 cuckoos were grey-white barred with blue-black, with odd black or white feathers; both the blacks and the cuckoos were shaded with brown as in the Houdan parent. Curiously, and unfortunately in some respects, the 6 blacks were all pullets and the 5 cuckoos all cockerels.

With regard to the black birds, the question naturally arose whether they were pure recessives RR or whether the usual dominant white character had receded, leaving them RD. In order to test this, the 5 black pullets were mated with a pure recessive black Houdan cockerel (mottled with white) (Experiment 15); eggs from this pen produced 48 chicks, all of which were black with white heads like the typical Houdan. These results show that the black pullets raised in Experiment 1 were in composition RR, for if they had been RD some dominant white chicks would surely have appeared in this experiment, when they were mated with a pure recessive.

[Note added December, 1904.

After this account was written one of the original white hens was found to have developed distinct colour-ticks in the hackles. To the impurity thus manifesting itself, the appearance of pure recessives in F_1 should, doubtless, be attributed.]

With regard to the nature of the exceptional cuckoo cockerels in Experiment 1, the experiments are not yet completed, though, so far, they have proved interesting, and bid fair to yield useful results. One of the cuckoo cockerels was mated with 2 of the black pullets; eggs from this pen produced 43 chicks, all of which had black down; 34 were ticked with white, 7 had white heads, and 2 were strongly shaded grey. All were more or less shaded with brown as in the Houdan; 31 of these were reared, and in their first plumage were 17 cuckoos and 14 blacks. Of the cuckoos 7 were cockerels and 10 were pullets, and of the blacks 8 were cockerels and 6 were pullets, so that the correlation of black with ♀ and cuckoo with ♂ in F_1 was not maintained in F_2.

The cuckoos were precisely similar to those of F_1, having a grey-white ground barred with blue-black, with odd black or white feathers. All had a distinct brown shade in the plumage. The blacks were of two types, dark Houdans and Crèves, suggesting that the cuckoo male parent was giving off black gametes. No dominant whites appeared in this mating, suggesting that the cuckoo male parent was *not* giving off dominant white gametes.

Further experiments are now in progress to carry this Mendelian analysis of the cuckoo cock a stage further, although an interesting complication has recently arisen in the fact that this bird has in his second plumage moulted out almost *clear white*, a single feather only, on the back, being slightly tipped with grey.

(3) *Feet.*

(*a*) All D's.

Gen.	Expt.	D.	R.
F_1	1	103	2
F_1	4	6	0
F_1	5	4	1
Total observations..		113	3
Mendelian calc. ..		**116**	**0**

(*b*) All R's.

Gen.	Expt.	D.	R.
F_1	2	0	57
F_1	3	0	60
F_1	6	0	107
F_2	8	0	119
F_2	10	0	56
Total observations ..		0	399
Mendelian calc. ...		**0**	**399**

(*c*) 3 D : 1 R.

Gen.	Expt.	D.	R.	Ratio.
F_2	7	179	47	3·8 : 1
Total obs.....		179	47	3·8 : 1
Mendelian calc.......		**169·5**	**56·5**	**3 : 1**

(*d*) 1 D : 1 R.

Gen.	Expt.	D.	R.	Ratio.
F_2	9	63	72	1 : 1·1
F_2	11	23	78	1 : 3·3
F_2	12	45	61	1 : 1·3
F_2	13	127	180	1 : 1·4
Total obs.....		258	391	1 : 1·5
Mendelian calc.......		**324·5**	**324·5**	**1 : 1**

In F_1 the extra-toe of the Houdan is dominant over the normal foot of the Leghorn, Hamburgh, and Cochin (Experiments 1, 4, and 5).

In some cases the dominance is complete, the extra-toe being reproduced in its entirety; in other cases the dominance is incomplete, all stages of extra-toe being produced from the almost perfect toe down to the mere duplication of the nail; in a few cases the e.t. (in all its stages) is found on one foot only, the other foot being apparently normal; in a few cases there is simply an elongated hallux.* A few apparent exceptions to dominance of e.t. occurred in Experiments 1 and 5.

In F_2 the hybrid dominant e.t.'s of F_1 mated together gave dominant e.t.'s and apparently recessive no e.t.'s in the proportion of 3·8 : 1 (Experiment 7); mated with pure recessive no e.t.'s they gave dominant e.t.'s and apparently recessive no e.t.'s in the varying proportions of 1 : 1·1 (Experiment 9), 1 : 1·3 (Experiment 12), 1 : 1·4 (Experiment 13), and 1 : 3·3 (Experiment 11).

The two exceptions to dominance in Experiment 1 of F_1 were fortunately of two sexes, and when mated together gave 22 chicks, of which 14 had e.t. and 8 with normal feet. The same cockerel was also mated with 4 Hamburgh-Cochin hens raised in Experiment 6, all, of course, with pure R normal feet, 24 chicks were raised, of which 11 had e.t. and 13 no e.t. The same pullet (Experiment 1) also gave some chicks with e.t. when mated with a pure Leghorn cockerel with R normal feet. These results prove that the apparently recessive feet with no trace of e.t. in Experiment 1 are in reality RD's, as both birds gave chicks with e.t. when bred together and with pure recessives. This is apparently a case where the usual dominant character has receded in F_1 to re-appear in F_2, and may safely be described as a true instance of the failure of dominance.† The fact of a recessive character, like normal foot, dominating occasionally in F_1 and proving in F_2 to be in reality RD is unfortunate, because it may lead to serious complications, *e.g.*, in Experiments 7, 9, 11, 12, and 13, noted above, we have no certainty that all the apparent recessives are RR's, as a few of them may be RD's, and if each bird with normal foot has to be tested individually in F_3 before it can be counted in F_2, it will be impossible to test the foot character on a statistical basis without great labour and expense, and it is quite possible that on account of this complication the foot character will have to be abandoned in future experiments, notwithstanding that in reality its inheritance may be in accordance with the Mendelian principles. Judging broadly from the above experiments in F_2, it is evident that the segregation is on Mendelian lines, the only notable exception being Experiment 11 where the ratio is 1 : 3·3 instead of the equality expected.

In this experiment, there is not only a large excess of recessives, but even the dominants are abnormal, tending towards the recessive character, for the majority of those with e.t. have it on one foot only, which is quite different from the normal result in all the other experiments, where the one-sided e.t.'s are in a small minority. These facts point to some abnormal disturbance in this experiment.

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* *Cf.* Bateson and Saunders, Report I (1902), p. 97.

† *Cf.* Bateson and Saunders, Report I (1902), pp. 102, 113, 115.

(4) *Shank-feathering.*

(*a*) All D's.

Gen.	Expt.	D.	R.
F_1	3	60	0
F_1	5	5	0
F_1	6	107	0
F_2	12	106	0
Total observations..		278	0
Mendelian calc. ..		**278**	**0**

(*b*) All R's.

Gen.	Expt.	D.	R.
F_1	1	2	108
F_1	2	0	57
F_1	4	0	6
F_2	7	7	219
F_2	9	0	135
F_2	11	0	101
Total observations ..		9	621
Mendelian calc. ..		**0**	**630**

(*c*) 3 D : 1 R.

Gen.	Expt.	D.	R.	Ratio.
F_2	8	115	4	28·7 : 1
Total obs. ..		115	4	28·7 : 1
Mendelian calc.		**89·2**	**29·7**	**3 : 1**

(*d*) 1 D : 1 R.

Gen	Expt.	D.	R.	Ratio.
F_2	10	35	21	1·6 : 1
F_2	13	195	112	1·7 : 1
Total obs. ..		230	133	1·7 : 1
Mendelian calc.		**181·5**	**181·5**	**1 : 1**

In F_1 the shank-feathering of the Cochin is dominant over the clear shanks of the Leghorn, Houdan, and Hamburgh (Experiments 3, 5, and 6). In all cases the dominance is incomplete, the length and number of the feathers being reduced to a fairly uniform one-half. No exceptions to this incomplete dominance were observed.

In F_2, the hybrid dominant feathered shanks of F_1, mated together, gave a large number of dominant feathered shanks, with a few recessive clear shanks (Experiment 8); mated with pure recessive clear shanks, they gave dominants and recessives in the proportion of 1·6 : 1 (Experiment 10) and 1·7 : 1 (Experiment 13). The Mendelian expectation for Experiment 8 was 3 D : 1 R, while the actual result was most exceptional, being, in fact, nearer 30 : 1 than 3 : 1.

The nature of the dominants, too, was different, for, while the Mendelian expectation was approximately 30 full-feathered and 60 half-feathered, the actual result was 17 full-feathered, 20 three-fourths, 57 half-feathered, 13 one-fourth, and 8 with feather traces. In fact, the dominants in F_2 represented a continuous series of feathering, ranging from full to clear, while in F_1 they were uniformly half-feathered. In Experiments 10 and 13 there was also continuous variation among the dominants, but the series only extended from one-half-feathered to clear, and the number of recessives was not far from the Mendelian expectation. From this it would appear that the Mendelian principles are at work in these aberrant phenomena, but are masked by something not yet perceived. It will be best, therefore, to reserve any attempt at explanation of them until the Mendelian analysis is completed in F_3.

Both in F_1 and F_2, among the recessive matings, a few slight traces of dominant feathering appear; these are apparently confined to Experiments 1 and 7, and, as similar traces appeared in the Houdan P_1, it is evident that the impurity came from that side, especially as it was never observed in the Leghorn.

One curious feature in this impure inheritance, is that in both experiments, where it showed itself, the actual parents did not show it, and, in the case of Experiment 7, neither the two parents nor the grandparents showed it, though the collaterals did ("uncles") (*cf.* Experiments 1 and 7). The impurity, therefore, seems to have remained latent for two generations in the direct line, though appearing in the collaterals.

Grand Totals (F_1 *and* F_2).

(*a*) All D's.

Characters.	D.	R.
Combs	437	0
Downs	499	26
Feet	113	3
Shanks	278	0
Total obs.	1327	29
Mendelian calc.	**1356**	**0**

(*b*) All R's.

Characters.	D.	R.
Combs	0	60
Downs	0	6
Feet	0	399
Shanks	9	621
Total obs.	9	1086
Mendelian calc.	**0**	**1095**

(*c*) 3 D : 1 R.

Characters.	D.	R.	Ratio.
Combs....	470	182	2·5 : 1
Downs ...	259	86	3·0 : 1
Feet	179	47	3·8 : 1
Shanks ...	115	4	28·7 : 1
Total obs.	1023	319	3·2 : 1
Mendelian calc. ...	**1006·5**	**335·5**	**3 : 1**

(*d*) 1 D : 1 R.

Characters.	D.	R.	Ratio.
Combs....	134	107	1·2 : 1·0
Downs....	252	262	1·0 : 1·0
Feet	258	391	1·0 : 1·5
Shanks...	230	133	1·7 : 1·0
Total obs.	874	893	1·0 : 1·0
Mendelian calc. ..	**883·5**	**883·5**	**1 : 1**

The adding together of the results of different characters in different experiments may not be strictly legitimate, but, as each character in each experiment has been first dealt with separately, and all the details which go to make up the totals have been given, the objections to this method are reduced to a minimum, and are far outweighed by the advantages of the large numbers thus made available.

In regarding the 5560 observations as a whole, one cannot but be impressed by the close approximation to the Mendelian expectation; at the same time, it must not be forgotten that, although most of the characters have appeared to segregate, in accordance with the Mendelian principles, we do not yet know that the extracted recessives are pure, nor do we know that the complete dominants consist of pure and impure in the Mendelian proportions; several generations will have to be bred before these questions can be definitely determined.

If, however, the experiments be taken as they stand, the close agreement with the Mendelian expectation cannot be without significance.

Summary of Conclusions from Experiments with Poultry.

(1) When certain pure breeds are mated with their own kind, certain structural and colour characters breed true to type; in some of these characters there is little or no variation, while in others the variation about the type is considerable.

(2) When these pure breeds are crossed with one another, certain of these characters are usually dominant over the corresponding character, which is recessive. Dominant characters are rose comb, white plumage, extra toe, feathered shanks, white and blue shanks, crested head, brown egg-colour and broodiness, while leaf and single comb, black and buff plumage, normal foot, clear shanks, yellow shanks, uncrested head, white egg-colour and non-broodiness are all recessive to the above corresponding dominants. In their turn, some of these recessives are themselves dominant over others, *e.g.*, leaf comb and black plumage are dominant over single comb and buff plumage, which remain recessive.

Dominance appears to be of two kinds, *Complete* and *Incomplete*. Complete dominants are practically indistinguishable from the pure dominants; incomplete dominants are variable, showing the influence of the recessive character in different degrees, the intensity of the dominant character being correspondingly diminished. In some character matings the dominance is apparently always complete, in some it is always incomplete, and in others it is sometimes complete, but more often incomplete. On the whole, the incomplete dominants appear to be about twice as numerous as the complete dominants. The pure recessive is always quite distinct from both kinds of dominants.

(3) When the offspring of the dominant first crosses are bred together, and with various dominants and recessives, some of their progeny exhibit the dominant, and others the recessive, character, the proportions of each being, as a rule, in close agreement with Mendel's

law. In these crosses the dominants are again complete and incomplete, the former being indistinguishable from the pure dominants, and the latter corresponding to the incomplete dominants in the first crosses with fair consistency. The recessives are, as a rule, similar to the original ones, but their purity has not yet been tested.

(4) No correlation was found between the comb, down, and foot characters, each, apparently, being a unit-character with an independent inheritance. When any two or three of these characters were considered together in individual birds, the numbers of each type in the second crosses approximated closely to the numbers calculated by means of Mendel's law.

(5) A few exceptions to the general results stated in (2) and (3) may be briefly noted: (*a*) a few recessives appeared in some of the first crosses instead of the usual dominants; these proved to be of two kinds, impure and pure, the former giving some dominants when mated with a pure recessive (p. 80), while the latter did not (p. 79). The appearance of a few impure recessives in the first cross indicates that the normally recessive character (normal foot) may sometimes dominate, which fact may lead to future complications. The pure colour recessives in F_1 are, without doubt, to be ascribed to impurity in a white parent, signs of which subsequently revealed themselves. (*b*) In all the second crosses, where buff plumage and shank-feathering were concerned, the variation of the offspring appeared to be much more continuous than in the corresponding matings of the first crosses. Experiments are in progress to test the nature of these exceptions by Mendelian analysis.

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REPORTS TO THE EVOLUTION COMMITTEE OF THE ROYAL SOCIETY.

Report III.

EXPERIMENTAL STUDIES IN THE PHYSIOLOGY OF HEREDITY.

By W. Bateson, M.A., F.R.S., Miss E. R. Saunders, Lecturer, Newnham College, and R. C. Punnett, M.A., Fellow of Gonville and Caius College, Cambridge, Balfour Student.

(Received March 16, 1906.)

CORRIGENDA TO REPORT II.

Page 12. In Exp. 18D, for "51" read "54."
„ 16. In Exp. 28B, for "67" read "64."
„ 18. In heading of table, for "*20a* and *20b*" read "30A and 30B."
„ 33. In left-hand column, for "18B, 19, 18A" read "28B, 29, 28A." and for "31" read "31C."
„ 46. In table, for "K" read "V_1."
„ 85. In I, for "Blanche Burpee × E. H. red," read "× E. H. round."
„ 117, line 8. For "× white" read "× coloured."
„ 121, line 11. For "Abyssian" read "Abyssinian."

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Introduction.

Grants received from the Government Grant Fund, and from the British Association, have been applied in part to the cost of the experiments upon which we now report, and in part to other researches which will be described hereafter. These sums would have been insufficient to enable us to carry on the work, and the scope of the investigation must have been greatly reduced had it not been for the generosity of Mrs. Herringham, who in 1904 placed a fund at our disposal for this purpose. We wish to record our deep sense of obligation to her for this assistance.

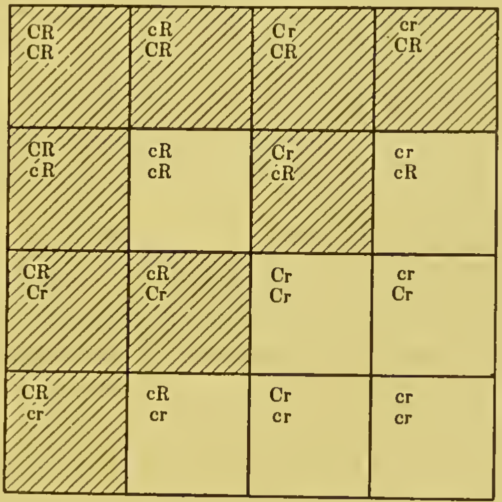
The results obtained since the last Report have at length provided expressions which include most of the phenomena witnessed in the case of Sweet Peas and Stocks. These various results can now be treated as parts of a consistent whole, and a great simplification of statement is thus made possible.

Flower-colour in Sweet Peas (LATHYRUS) *and Stocks* (MATTHIOLA).

The phenomena in these two plants are essentially similar in that (1) a purple F_1 results from a cross between certain white* varieties; (2) F_2 consists of purples, reds, and whites. In each case subordinate colour-classes are present among the purples and among the reds. These minor distinctions are for the present disregarded.

The facts show that the appearance of colour is due to the association, in one zygote, of two factors belonging to independent allelomorphic pairs. The presence of either factor alone is insufficient to cause colour in the zygote. One of the two factors was brought in by each original parent.

Speaking of the two factors as C and R, the corresponding allelomorphs are respectively *c* and *r*, the absence of those factors. When all the combinations of two such allelomorphic pairs are represented in F_2, there will, among 16 individuals, be on an average 9 in which both factors are present, and 7 having only one or neither of them, as shown in the accompanying scheme (fig. 1).



▨ CR CR	▨ cR CR	▨ Cr CR	▨ cr CR
▨ CR cR	cR cR	▨ Cr cR	cr cR
▨ CR Cr	▨ cR Cr	Cr Cr	cr Cr
▨ CR cr	cR cr	Cr cr	cr cr

FIG. 1.—Diagram showing the nature of the ratio 9 : 7 in F_2. The character, colour for example, appears only when C and R meet. Each square is a zygote, and the lettering shows its gametic composition. The hatched squares represent coloured plants; the plain are whites.

The 9 will be coloured, the 7 will be white. There will be 4 gametically distinct types among the coloured and 5 among the whites. Many of these extracted types have already been recognised experimentally.

---

* White here means non-sap-coloured. In the Sweet Peas the two parent forms were white with long pollen, and white with round pollen. In the Stocks the corresponding parent types were white glabrous and cream glabrous. The cream-colour is due to the presence of yellowish plastids, a character recessive to colourless plastids. This feature is quite distinct from sap-colour, and, in that respect, creams are true whites.

The ratio of coloured to white is thus 9 : 7. The coloured, however, consist of two main classes, purples and reds, in the ratio 3 purple : 1 red. The ratio of the three classes is therefore 27 purple : 9 red : 28 white. Such a distribution evidently results from the presence of a third allelomorphic pair, B, *b*, the presence or absence of a *blue* factor, which is dominant over the redness; but this only produces a perceptible effect when both C and R are also present. The relation of their distribution to the ordinary tri-hybrid scheme may be shown thus—

$$\underbrace{27 : 9}_{\substack{36\\9}} : \underbrace{9 : 9 : 3 : 3 : 3 : 1}_{\substack{28\\7}}$$

In the Sweet Peas it is clearly the long-pollened white which introduced the factor B; for when crossed with red types it gave purples, whereas the round white gave reds in such crosses. The occurrence on one occasion of red bicolor, the "half-reversion" of Rep. II, p. 84, in F_1 from long white × round white, was due to the circumstance that the particular long white used had no B factor (*cf.* scheme, p. 10).

In Stocks this factor was introduced by the *white* glabrous Stock, not by the cream glabrous; for F_1 from white × red is purple, but F_1 from cream × red is red (see p. 6).

Some outstanding problems are presented by the sub-classes of purples and of reds, which exist in both the Sweet Pea and the Stock F_2 families. Several of these differences depend on the presence of other simple allelomorphs, and are merely superposed on the primary classes, while others are of a more complex nature, which is not yet understood.

The fact is remarkable that in both Stocks and Sweet Peas certain lighter colours are dominant to the darker, in the sense that in families containing both, the darker can be bred from the lighter, while the contrary is impossible.

Thus in the Stocks light purple is to dark purple what in Sweet Peas the reversionary purple with blue wings is to the purple with purple wings; and light red or "flesh"-coloured are to the full red Stocks what the Painted Lady Sweet Pea with light wings is to the Miss Hunt form with magenta wings.

Certain cases in which a *coloured* type was used as an original parent gave results which cannot yet be brought into harmony with this scheme, but the majority now present no difficulty.

The results here summarised agree well with those obtained by Tschermak in Phaseolus, where a somewhat similar case of reversion in

F_1 was studied. The chief difference lies in the fact that in our case the original parents were both white.

Mutatis mutandis, Correns' case in *Mirabilis* presents many points of similarity, but in that plant the pigmentary substances are evidently different.

The phenomena described (Rep. II, pp. 44 to 53) in *Salvia Horminum* are now obviously reducible to the same system, and the figures which we took to represent the ratio 2 : 1 : 1 are in reality* examples of 9 : 3 : 4. It is likely that all plants possessing similar sap-coloured varieties will be found to conform to this scheme. We note, however, that in *Primula Sinensis* (unpublished results of R. P. Gregory) blue has been shown to be recessive, and presumably, therefore, the nature of the pigmentary substances is different.

It is premature to discuss the physiological nature of the two factors which, when they meet, produce colour, but it is not inconceivable that they may yet be isolated.

HOARY LEAVES IN STOCKS.

The character hoariness in Stocks is similarly due to the simultaneous presence of two independent factors which we shall call H and K, allelomorphic to *h* and *k*, the absence of those factors. The F_2 results show that, generally speaking, hoariness, the result of the interaction of H and K, cannot be produced unless C and R, the colour-factors, are also present. The existence of *white*-flowered hoary strains creates a difficulty. As regards "white" *incana*, this difficulty is only apparent, for it is certain that "white" *incana* is in reality a coloured form. Its flowers tinge on fading, and its embryos have the deep green colour characteristic of purple-flowered types. The white hoary Bromptons, however, are a marked exception to the general rule. Their flowers are not in any way coloured, and their seeds have at most a slight green tinge (sometimes none). Bromptons have been little studied in these experiments, and as yet we have no clue to the nature of their peculiarity.†

In a few cases (see *e.g.*, Exp. 28 B) there are rather wide departures from the F_2 numbers indicated by this scheme, and it is no doubt just possible that these figures indicate some further complication. With these exceptions, there is now a satisfactory account of all the chief phenomena, many of which were previously quite paradoxical. For example, we had found that

---

* For instance, Experiments 16 and 17 (Report II, p. 50) give in F_2 respectively 59 purple, 25 pink, 34 white, and 255 purple, 92 pink, 114 white; together, 314, 117, 148, when the expectation is 324, 108, 144. Similarly, Experiment 13 gave F_2 26 purple, 17 white. At that time equality was the supposed expectation, and the excess of purples was remarked on: There can now be no doubt that the true ratio was 9 : 7, which would give 24·2 and 18·8.

† As white Bromptons × cream glabrous give red F_1, it is evident that they do not carry B.

	1.	Cream	glabrous	×	white	glabrous	gave	purple	hoary.
	2.	,,	,,	×	purple	,,	,,	,,	,,
	3.	,,	,,	×	red	,,	,,	red	,,
	4.	White	,,	×	purple	,,	,,	purple	,,
	5.	,,	,,	×	red	,,	,,	,,	,,
but	6.	Any red or purple	,,	×	any red or purple	,,	,,	red or purple	} *glabrous.*

These facts were not consistent with the simple supposition that cream, for instance, bore a factor α, which, when it met a factor β borne by, say red, gave hoariness. For since *white* × red also gives hoary F_1, the white must similarly bear α; but though on this reasoning white and cream are alike bearing α, yet when crossed they also give hoary F_1. The explanation is that the types have the following composition :—

White glabrous………	H and K	C or R
Cream ,, ………	H and K	R or C
Purple ,, ………	H or K	C and R
Red ,, ………	H or K	C and R

Moreover, the whites and purples carry B, while the creams and the reds are without this factor.

That this is the true account appears from the distribution of characters in F_2. From cream glabrous × white glabrous, F_2 consists of coloured *which are all hoary*, and whites and creams *which are all glabrous*. When, however, cream or white glabrous is crossed with a sap-coloured glabrous, all the hoary are coloured in F_2; but of the glabrous some are coloured and some are white.

Again, F_2 from "white" *incana* × sap-coloured glabrous, contains *tinging whites* in both hoary and glabrous classes.

From these considerations it follows that hoary F_2 plants may be of three kinds—(1) those which give all hoary in F_3; (2) those that give 9 hoary to 7 glabrous; (3) those that give 3 hoary to 1 glabrous. All these kinds have been experimentally recognised (see p. 41).

"LATENCY"; RESOLUTION; DETERMINING FACTORS.

Cuénot showed that when in mice a new colour appears in F_1 from colour × albino, this is due to the introduction by the albino of a factor which, when it meets the colour brought in by the coloured parent, modifies it. For instance, when black × white gives grey (*i.e.*, wild colour) F_1, this is due to a grey determining factor, brought in by the albino, meeting the colour brought in by the black. The grey determiner thus dominates over the black determiner to which the original black owes its blackness; and F_2 will be 9 grey, 3 black, 4 albino. Cuénot represents the allelomorphic pairs as—

Colour (C).	No colour (A).
Grey determiner (G).	Black determiner (B).

More strictly, perhaps, we think they may be represented as

Colour (C).	Absence of ditto (c.).
Grey determiner (G).	,, ,, (g.).
Black ,, (B).	,, ,, (b.).

The arithmetical results are, of course, the same.* In the case just mentioned both parents can be regarded as homozygous in B, while the albino is also homozygous in G. But when grey × albino gives in F_2 3 grey : 1 albino, the fact that no new colour appears is due to the circumstance that the albino is homozygous in G. When the same cross gives in F_2 9 grey, 3 black, 4 white, the occurrence of the blacks proves that the albino carried no G, and that both the original parents were homozygous in B.

Albinos extracted from blacks cannot be bearing any determiner dominant to B; and if the blacks give no colours but blacks (and albinos), then the albinos so extracted must be homozygous in B, although they may still carry determiners recessive to B—that of chocolate, for example. If the allelomorphic pairs are expressed in the way indicated, the relation of the plant to the animal cases becomes clear.

Analysis of this kind is applicable to many and perhaps to all of the phenomena which we have hitherto attributed to resolution of a compound allelomorph, though as now appears they are merely expressions of a simple Mendelian process. The polymorphic F_2 of Sweet Peas and Stocks is now almost entirely reducible to terms of the same simple system.

Animal and plant cases differ remarkably in the fact that in animals colour has not yet been shown to be due to the meeting of two complementary factors. For no instance is known of two albino animals giving coloured F_1; and similarly the ratio 9 coloured : 7 albino has not been met with in any F_2 from coloured × albino in animals, though in plants such cases are not now very rare. Consequently, if in animals colour does depend for its appearance on two complementary factors (apart from *determining* factors, which exist in plants and animals alike), it must be recognised either that they have never separated, or, as is more probable, that one of them is present in all individuals, whether coloured or albino. Animals have probably reached the stage in which one only of the two factors may be absent, whereas in some plants both may be absent from the gamete.

---

* The correctness of this representation can be tested by crossing a wild grey mouse with a chocolate. If the view here expressed is right, *blacks* must appear in F_2.

A character such as colour, depending on double factors, or hoariness in Stocks, produced by four factors, may no doubt be properly spoken of as a compound character, and so we may speak of its "resolution," but in a sense different from that we originally intended. The compound is now seen not to be, in its entirety, a unit allelomorphic to another unit-character, but to be made up of several characters, each belonging to an independent allelomorphic pair. Consequently, in these cases, the conception of synthesis becomes superfluous; for the fact that a new type appearing in F_1 may breed true after F_2 is now shown to be an ordinary phenomenon of homozygosis.

Castle and others have spoken of the presence of a determiner, *e.g.*, that for black, in the albino, as a "latency" of black in the albino. It should, however, be realised that it is not "black" as a whole which is latent. One of the factors needed to produce black is present—as a cryptomere, to use Tschermak's term—which cannot be made perceptible unless it meets colour in the zygote.

REVERSION.

The conception of reversion on crossing now takes a definite shape. Such reversion is simply the reappearance of a feature which had disappeared owing to the absence of one of the complementary factors. When 2 white Sweet Peas give a red bicolour F_1 there is reversion to the old "Painted Lady" type, because the two factors necessary for the development of that colour meet again. When the reversion is "total" (see Rep. II, p. 84, etc.) and F_1 is purple, the same two factors meet in the presence of the third element B, the determiner for purple. So for reversion in Stocks: when C meets R, the two whites give red F_1; if B is likewise present, a purple F_1. If both H and K, brought in by 2 glabrous types, meet in the presence of C and R, the further reversion to the hoary structure occurs. Somewhere in the history of the evolution of the modern types, the complementary elements have been split off and eliminated, giving rise to analytical variations.

GAMETIC COUPLING.

Early in the revival of breeding experiments, attention was called, especially by Correns, to the phenomenon of coupling between characters. Complete coupling has so far been most commonly met with among characters of similar physiological nature. Examples of complete coupling between characters apparently quite distinct in nature are less frequent. As an illustration, we may refer to the apparently universal association of procumbent habit with dwarf stature in Cupid Sweet Peas, though in Pisum there is no such association between dwarfness and procumbency.

Examples of *partial* coupling have not hitherto been adequately studied. A remarkable case occurs in regard to the distribution of the pollen-characters in F_2 from the white long × white round Sweet Pea. There is here a partial coupling between the purple flower-colour and the long pollen. The whole mass of F_2 consists of 3 long : 1 round. The whites taken alone are also 3 long : 1 round. The *purples*, however, show a great preponderance of longs over rounds, about 12 to 1, while among the *reds* the rounds are in excess over the longs, being about 3 to 1. These peculiar distributions only occur in families which contain both red and purple members. Families (in F_3, for example) consisting of purples alone, or of reds alone, or of either associated with whites, have normal compositions. Evidently the abnormal distribution in some way depends on the mode of segregation of the factors B and b from each other. A close approach to the observed F_2 numbers would be given by a system in which each 16 gametes were composed, thus :—

$$7\mathrm{AB} + 1a\mathrm{B} + 1\mathrm{A}b + 7ab,$$

where A is long pollen and a round pollen,

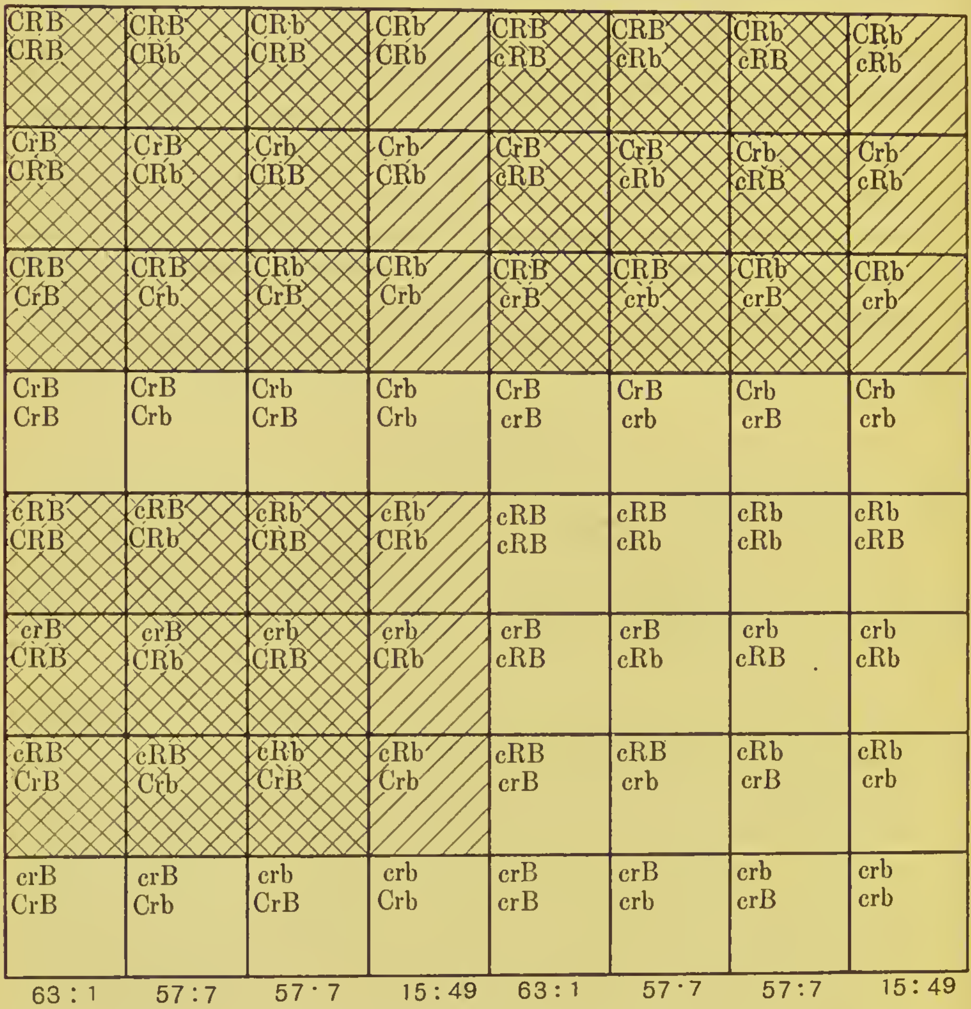
	Purple.		Red.		White.	
	Long.	Round.	Long.	Round.	Long.	Round.
Observed	1528	106	117	381	1199	394
Calculated	1448·5	122·7	122·7	401·5	1220·5	407·4

The distribution of the various characters may then be represented by the accompanying diagram (fig. 2), p. 10.

The significance of such partial coupling is obscure, and it may result from several processes, between which no discrimination can yet be made. Nothing *a priori* limits us to the view that all characters are segregated at one division, but no system of symmetrical dichotomies will give the 7 : 1 system. If, however, the gametes AB and ab belonged to a generation later than aB and Ab, and were produced by three divisions after segregation had taken place, the numbers 8AB + 1aB + 1Ab + 8Ab would result. Our statistics are not large enough to decide positively between 7 : 1 and 8 : 1, though the former ratio fits best. There is no proof that all gametes of one flower are of the same order or generation counting from the fertilised egg, and, for example, we may feel sure that the male and female cells at least belong to different generations. Such a conception would introduce great complexity into these analyses, and in particular we should have to forego the natural view that segregation occurs at the reduction-division. There is another way in which the numbers 7 : 1 might be produced. If it were assumed that two other pairs of unknown factors X, x, Y, y were also present, and that the character A is always coupled with either X, Y, or B, the result would be that the series of 16 gametes would consist of

$$7AB + 1aB + 1Ab + 7ab.$$

All the characters would then be distributed in one dichotomy, and the



CRB CRB	CRB CRb	CRb CRB	CRb CRb	CRB cRB	CRB cRb	CRb cRB	CRb cRb
CrB CRB	CrB CRb	Crb CRB	Crb CRb	CrB cRB	CrB cRb	Crb cRB	Crb cRb
CRB CrB	CRB Crb	CRb CrB	CRb Crb	CRB crB	CRB crb	CRb crB	CRb crb
CrB CrB	CrB Crb	Crb CrB	Crb Crb	CrB crB	CrB crb	Crb crB	Crb crb
cRB CRB	cRB CRb	cRb CRB	cRb CRb	cRB cRB	cRB cRb	cRb cRb	cRb cRB
crB CRB	crB CRb	crb CRB	crb CRb	crB cRB	crB cRb	crb cRB	crb cRb
cRB CrB	cRB Crb	cRb CrB	cRb Crb	cRB crB	cRB crb	cRb crB	cRb crb
crB CrB	crB Crb	crb CrB	crb Crb	crB crB	crB crb	crb crB	crb crb
63 : 1	57:7	57·7	15:49	63:1	57·7	57:7	15:49

FIG. 2.—Scheme of distribution of colour-factors in F_2. From E. Henderson (Sweet Pea), white, long pollen × white, round.

The table is an expansion of that shown in fig. 1, and exhibits the effect of the blue factor, B. The cross-hatched squares are purple-flowered plants; the single-hatched are red; the plain are whites.

The figures at the foot of each column show the ratio of long-pollened to round-pollened in each square of that column, on the hypothesis given in the text.

apparently partial operation of the coupling would be elucidated. The difficulty in the way of this suggestion is that no characters corresponding with X and Y have yet been identified which fulfil the required conditions.

This discussion cannot now be carried further. It is clear that gametic coupling, however caused, plays a large part in the phenomena of heredity. As another illustration of the coupling of a structural with a pigmentary character, we may mention that in some strains of Sweet Pea (to be described hereafter) the hooded standard is coupled with certain types of flower-colour; being, so far as we have seen, never found in purple—or red—bicolours. Presumably, the facts related in Rep. II, p. 91, indicate a similar partial coupling between the light axil and the peculiar contabescence of anthers.

Zygotic Coupling must be carefully distinguished from gametic. A character may be developed in those zygotes alone which possess some second character; but in the system of gametic distribution of the allelomorphs there may be no coupling between the two characters. For example, when the peculiar yellow flush is developed in the petals of a plant of *Primula Sinensis* which bears the minute pollen of the long-styled type, the style does not rise above the anthers, constituting the "homostyle" condition.* Such plants are homozygous in respect of yellow flush and long-style pollen, but the two characters are entirely independent in their gametic distributions, as is proved by F_2 from homostyle × short style. Some very important illustrations of zygotic coupling are provided by the characters that are peculiar to one or other sex in sexually dimorphic species.

POULTRY.

(Experiments by W. Bateson and R. C. Punnett.)

Comb Characters.

Relation of Rose-comb to Pea-comb.

In our last Report (p. 112) we showed that, judged by the criterion of gametic output, 4 kinds of r.p. birds exist, viz., r. × p., r.p. × r.p., r.p. × r., and r.p. × p. Birds of the constitution r. × p. gave, on mating with single comb, equal numbers of the 4 types r.p., r., p., and s. Birds of the constitution r.p. r. and r.p. p. gave when crossed with s. equal numbers of r.p. and r., and of r.p. and p. respectively, whilst a pure r.p. bird gave only r.p. when similarly crossed. We suggested that a fifth type of r.p. bird was conceivable, *i.e.*, one giving off equality of r.p. and s. gametes. In order to test this possibility a pure r.p. ♀ was mated with a single comb ♂ (Experiment 268). Three ♀s. resulting from this cross were in the following year mated with their father (Experiments 342 and 343). From these matings all the 4 types of comb resulted. In other words, the gametic output of birds produced by the union of r.p. with s. cannot be distinguished from that of birds produced by mating r. with p. Judged, therefore, by gametic output, only 4 types of comb are known to exist.

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* W. Bateson and R. P. Gregory, 'Roy. Soc. Proc.,' 1905, vol. 76, p. 581.

Since the publication of the last Report we have been led to alter our views as to the nature of the r.p. comb, and have recently pointed out* that the case may be looked upon as one of simple dihybridism. On this view the allelomorphic pairs are (1) Rose and no-rose; (2) Pea and no-pea—the first member of the pair being in either case dominant to the second. The rose-comb is, therefore, in constitution Rose + no-pea (*R. no P.*) and the pea-comb Pea + no-rose (*P. no R.*). Consequently the zygote formed by the union of r. and p. has the constitution *R. no P. : P. no R.*, and the appearance of the walnut form must be regarded as due to the presence in the zygote of the 2 unit characters *R.* and *P.* which belong to distinct allelomorphic pairs. From such a zygote 4 sorts of gametes must be produced in equal numbers, viz., *R.P.*, *R. no P.*, *P. no R.*, and *no R. no P.* Since the single on this view must be homozygous and producing gametes of the constitution *no R. no P.*, it follows that an *r.p.* bird such as we are considering will, when mated with a single, give rise to 4 zygotic types in equal numbers. Constitutionally these will be (1) *R. no R. : P. no P.*, (2) *R. no R. : no P. no P.*, (3) *P. no P. : no R. no R.*, and (4) *no R. no R. : no P. no P.*, and visibly such birds will be *r.p.*, *r.*, *p.*, and *s.* respectively. Again, when mated together, 2 such *r.p.* birds will produce *r.p.*, *r.*, *p.*, and *s.* birds in the ratio 9 : 3 : 3 : 1. The constitution of such birds is set forth in the accompanying table (p. 13), which shows that the r.p. birds may be of 4 sorts, viz. (1) homozygous for both *R.* and *P.*; (2) homozygous for *R.* and heterozygous for *P.*; (3) homozygous for *P.* and heterozygous for *R.*; and (4) heterozygous for both *R.* and *P.* The relative proportions of birds belonging to the 4 classes (1), (2), (3), and (4) will be 1 : 2 : 2 : 4. As the table shows, one of the 3 roses and one of the peas will be homozygous.

We have already pointed out† that the proportion of the different combs in the various matings affords no criterion for judging between this view and the one previously suggested. The new view, however, explains the identity of the combs produced by the crossing of r. with

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* 'Proc. Camb. Phil. Soc.,' 13, p. 167.

† *Loc. cit.*

p. and of r.p. with s., thus dispensing with the conceptions of compound allelomorphs and synthesis.

RP RP (r.p.)	RP R, no P (r.p.)	RP no R, P (r.p.)	RP no R. no P (r.p.)
R, no P RP (r.p.)	R, no P R, no P (r.)	R, no P no R, P (r.p.)	R, no P no R, no P (r.)
no R, P RP (r.p.)	no R, P R, no P (r.p.)	no R, P no R, P (p.)	no R, P no R, no P (p.)
no R, no P RP (r.p.)	no R, no P R, no P (r.)	no R, no P no R, P (p.)	no R, no P no R, no P (s.)

During the past two years we have tested a considerable number of r.p. combs, with the result that each of the 4 types has been met with over and over again. Speaking generally, this form of comb exhibits much variation in size, shape, and amount of the special feathering on its posterior surface, though hitherto we have been unable to establish any connection between such variations and the gametic output of individuals in which they occur.* We may now consider in rather more detail the matings in which the various types of r.p. combs are concerned.

Pure r.p. (zygotic constitution *R.P.R.P.*).—This type has occurred in 2 Malay bantam hens (Experiments 242, 268, 284) and in a black-red Malay ♂ (Experiment 351) all purchased. It has also occurred in F_2 from an original cross of r. × p. (Experiments 255, 256, 333, 383). Further, we have one case (Experiment 366) where it was formed from 2 r.p. birds which were produced by the mating of r.p./p. with single. Since every bird with an r.p. comb must give off some gametes at any rate containing both *R.* and *P.*, we may, of course, expect some pure r.p. birds to be produced by the mating of any 2 birds with this form of comb. In all the above experiments r.p. combs alone resulted from the union of the pure r.p. bird with a single.

Combs r.p. × p. (zygotic constitution *R.P.P. no R.*).—(*Cf.* Experiments 196 to 197, 239, 271, 278, 287, 305, 314, 328, 336, 355, 357 to 358, 385, 387 to 388, 390, 391.)

The birds tested in Experiments 196 to 197, 239, and 287 were Malays with natural r.p. combs. The rest were produced artificially in F_2 from original matings r. × p., r.s. × p.s., or r.p. × s. On mating with singles this type of r.p. comb gave in all 285 r.p. and 296 peas, the expectation, of course, being equality.

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* *Cf.* Report II, p. 112.

Combs r.p. × *r.* (zygotic constitution *R.P.R. no P.*).—(*Cf.* Experiments 233, 283, 297, 316, 338 to 339, 360, 371 to 372.)

The bird tested in Experiment 283 was a ♂ Malay bantam, whilst those in Experiments 233 and 316 were Malay ♀s. The rest were artificially produced. Altogether 289 birds were produced, of which 149 had r.p. and 140 rose-combs, expectation as in the last case being equality.

Combs giving all 4 with Single (zygotic constitution *R. no P. P. no R.*).—(*Cf.* Experiments 208, 212 to 214, 217 to 218, 232, 234, 236, 238, 240 to 241, 243, 249, 251 to 252, 260 to 262, 272, 275, 277, 298, 300, 302 to 303, 306 to 307, 309, 311 to 313, 315, 317 to 320, 323 to 327, 329, 331 to 332, 334, 342 to 343, 345 to 348, 359, 361 to 365, 373 to 374, 382, 386.)

Of the 1,251 birds produced in the above experiments 373 were r.p., 425 pea, 413 rose, and 440 single, expectation in each case being 413. There is a marked deficiency of r.p. and a distinct excess of singles. These disturbances in the expected ratio of equality we are inclined to attribute to the behaviour of the 4 ♂s. used in Experiments 306, 347 to 349, and 373 to 374—cases which must be considered in rather more detail.

The ♂s. in Experiments 306 and 349 gave only 10 r.p. birds out of a total of 93, *i.e.*, only half the number expected, although the total number of chicks hatched was fairly large. These cases were not followed up, but when the same phenomenon reappeared in Experiment 373, the ♂ bird was mated also to 4 pure Br. L. ♀s. (Experiment 374). Again, there was a marked deficiency of r.p. chicks, pointing to something unusual happening among the gametes of this ♂. The bird has been kept in order that further experiments may be made next year.

Experiments 347 to 348 seem to point to a disturbance of a somewhat different nature. The ♂ (No. 144 of 1904) was originally mated with 3 single combed ♀s. to test the nature of his comb. Later on a black Andalusian ♀ and 2 Wh. L. ♀s. were introduced. The ♂ turned out to be giving off all 4 kinds of gametes, giving with the 3 original ♀s. and the black Andalusian 18 s., 26 r., 26 p., and 25 r.p. With the 2 White Leghorn hens, however, he gave an extraordinary deficiency of r. and r.p., the numbers being 17 s., 2 r., 17 p., and 3 r.p.

In the case of each of these 4 birds the numbers are so aberrant that we can for the present hardly avoid regarding them as due to some disturbing circumstances. The number of chickens involved is 309, viz., 107 s., 75 r., 86 p., and 41 r.p. Subtracting these numbers from the sum totals given above, we are left with 333 s., 338 r., 329 p., and 332 r.p., which is a very close approach to the expected ratio of equality.

Rose Pea-combs Mated Together.

Zygote *R. no P. P. no R.* × zygote *R. no P. P. no R.* In the last Report (p. 110) were mentioned four experiments of this nature in which the figures obtained were not far removed from the expected ratio of 9 : 3 : 3 : 1.

Further experiments of the result of this type of mating were made in 1904, and are set out in the table below :—

	s.	r.	p.	r.p.
Experiment 201	2	5	7	16
„ 202	2	5	9	8
„ 204	10	5	4	15
„ 205	2	9	8	22
„ 206	2	4	5	9
„ 215	4	19	19	33
„ 216	2	4	5	11
„ 244	—	—	2	2
„ 245	1	5	4	13
„ 253	6	8	14	36
„ 254	3	5	9	12
	34	69	86	177
Expectation	22·9	68·7	68·7	206·1

The result discloses a distinct excess of singles and peas, together with a deficiency of r.p.s. Examination of the table shows that whilst the result in certain cases (*e.g.*, Experiments 201, 205, 216, 245) fits closely with expectation, it is in other cases far removed from it. Thus in Experiment 204 we should have expected not more than 2 singles, whereas the actual number is 10. Yet the subsequent Experiments 212 and 300 prove that the ♀ was then giving off all four sorts of gamete in equal numbers, whilst Experiments 208 and 303 show that the same was also true of the ♂. It is conceivable, of course, that the numbers in Experiment 204 may be the result of chance, but, having regard to the fact that wherever any serious disturbance of the ratio 9 : 3 : 3 : 1 occurs it is generally accompanied by both excess of singles and deficiency of r.p.s., we are more inclined to attribute such aberrations to the presence of some disturbing circumstance hitherto undetermined.

"Extracted" Combs from mating r.p. × r.p.

Singles "extracted" from the cross r.p. × r.p. were mated together in Experiments 209, 210, 247, and 248. Of the 144 chicks resulting, all were single.

Seven extracted roses were tested, with the result that one turned out to be homozygous (Experiment 273) and the rest heterozygous (Experiments 246, 263 to 6, and 274). With single combed ♂s. these 6 birds produced 176 chicks, of which 92 were single and 84 rose. Extraction has clearly no influence upon the behaviour of rose and single combs.

An extracted ♂ pea-combed bird produced (in Experiment 230) 2 singles and 3 peas with a Br. L. ♀. In Experiment 231 an extracted pea-combed ♀ gave, with an s.c. ♂, 5 singles and 8 peas. In Experiment 228 an extracted p.c. ♂ was bred with 3 extracted p.c. ♀s., and gave 20 singles to 34 peas, the expectation being 13·5 : 40·5. Such an aberration from the expected ratio may easily be the result of chance, though it is possible that it may be due to the prevalence of intermediate pea-combs.

Intermediate Pea-combs.—In certain families where the pea-comb was concerned, heterozygote (p.s.) birds occurred with some frequency showing so little of the pea character that as young chicks they could easily be taken for singles. The median ridge is very high, approaching the single comb, whilst the lateral ridges are much reduced. Such a comb requires very close scrutiny in the newly hatched chick to distinguish it from a single. In one case such a bird, recorded as a single when a chick, eventually grew up with one of these intermediate pea-combs. Experiments with reference to the nature of this comb are still in progress, and until they are complete we propose to defer our detailed account. We have alluded to the case here because it may have some bearing on the excess of singles in Experiments 231 and 357. At the time of that experiment we had not fully grasped the distinction between the intermediate pea and the single comb, and it may very well be that some of the combs then recorded in certain families as single were in reality of the intermediate type.

The Malay Comb.

In the last Report (p. 111) we drew attention to the paradox that real rose and single combs are not known to occur among Malays when bred pure, and we suggested as a possible explanation that the ♂s. only are capable of producing all four forms of gamete. In a subsequent note (p. 112) we alluded to a ♀ Malay which was recorded to have given (with a single combed ♂) 2 s.c., 1 r., 1 p. and 1 r.p. This ♀ was again tested in 1905 (Experiment 334) and gave with a Br. L. ♂ 7 s., 2 r., 2 p., and 3 r.p. There is, therefore, no doubt that ♀ Malays as well as ♂s. can give off all four kinds of gamete. Unfortunately we were unable to procure a ♂ Malay of this nature in 1905, and the absence of roses and singles in pure Malays must, for the present, remain unexplained.

Colour.

White × *Colour.*—The experiments described in the last two Reports have already shown that white behaves as a dominant to colour, and the evidence obtained in the past two seasons confirms this. Four extracted whites, viz., ♀ 463 (Experiment 196), ♀ 425 (Experiments 214, 238, and 251), ♂ 375 (Experiments 273, 274), and ♂ 415 (Experiments 338 and 339) were shown to be homozygous. Matings of the nature DR × DR are shown in the following table:—

	Light.	Coloured.
Experiment 204	31	3
,, 205	35	6
,, 206	17	3
,, 211	209	57
,, 212 ,, 300	21	7
,, 220	11	3
,, 299	186	58
,, 307	56	24
	566	161
Expectation	545	182

There is a slight deficiency of coloured birds due in part to the small number produced in Experiments 204 to 206 where 3 ♀s. resulting from a cross between Wh. Dork. and I. G. were mated with their brother. In part also the excess of lights arises from the occasional difficulty of distinguishing at the hatching stage between a chick which will grow into a pile (viz., orange-red and white) from one which will develop into a white. Usually the pile is slightly marked with buff on the head or elsewhere, but in cases where the eggs were opened a day or two before hatching, or where the chick died in the shell, this buff might easily be overlooked, and the chick in consequence registered as uncoloured. Indeed, such a case actually happened, a bird recorded as uncoloured in down on being reared turning out to be a pile. We believe that the deficiency of coloured birds in Experiment 211 is due to this cause, for on repeating the experiment in 1905, and paying particular attention to this point, the expected proportion of coloured birds appeared.

The matings of DR birds with RR gave on the whole a fairly close approach to the expected ratio of equality. As the table shows (see p. 20), irregularities occur here and there, but whether these are merely fortuitous we cannot at present say:—

	Light.	Coloured.		Light.	Coloured.
Experiment 203 ...	3	4	Experiment 310 ...	9	12
„ 207 ...	8	4	„ 311 ...	13	15
„ 213 ...	10	14	„ 312 ...	6	7
„ 221 ...	9	7	„ 315 ...	3	4
„ 223 ...	27	36	„ 316 ...	5	5
„ 232 ...	11	20	„ 317 ...	8	7
„ 233 ...	2	9	„ 318 ...	11	6
„ 240 ...	8	11	„ 319 ...	1	—
„ 247 ...	19	13	„ 320 ...	15	13
„ 249 ...	5	4	„ 324 ...	18	31
„ 259 ...	25	15	„ 325 ...	4	4
„ 301 ...	5	19	„ 383 ...	7	4
„ 302 ...	5	7	„ 384 ...	2	8
„ 304 ...	2	2	„ 385 ...	7	8
„ 308 ...	5	4	„ 386 ...	4	3
„ 309 ...	14	14	„ 390 ...	10	13
	158	183		123	140
				158	183
			Total	281	323
			Expectation	302	302

Recessive Whites.—One of the most interesting features of the past two years' work has been the demonstration of the existence of two sorts of white birds. To the first class belong the whites which we have just been considering. These behave as dominants to colour, and may for convenience be termed D-whites. The second class behave as recessives to colour, and may be spoken of as R-whites. Such R-whites we have already found in several breeds of fowls, viz., in Rosecomb bantams, Wyandottes, Dorkings, and Silkies. It is possible that a White Leghorn ♀ used by Hurst in one of his experiments (Rep. II, p. 134, Experiment 2) was also of this nature. These R-whites *are characterised by the possession of a few minute ticks in their otherwise pure white plumage,* a feature which we have already mentioned in the case of the white Rosecomb bantam (*cf.* Rep. II, p. 117, note). These minute ticks we have also found in white Wyandottes and in Silkies. Such evidence on the nature of the R-white as we have up till now collected may be conveniently considered under the headings of the different breeds which we have used.

(α) *Rosecomb Bantams.*—Two pens of whites (Experiments 280 and 290) bred in 1904 were proved to come true to colour. The down colour of the chicks was very pale bluish white, not unlike that of the white-splashed Andalusians. In Experiment 279 a few chicks were produced from a pen of blacks. The down colour of these was similar to that found in other black breeds, viz., black with white ventral surface. In

1905 crosses were made between black and white (Experiments 350, 356, 369), and all the resulting 88 chicks were black in the down. Certain of these have been reared, and in their adult plumage are either pure black or black with some white spangling. The spangling is probably a separate character with an independent inheritance. White Rosecomb ♂s. were also crossed with a coloured ♀ bantam* of unknown origin (Experiment 291), and an F_2 game bantam produced in Experiment 267. In both cases all the chicks were coloured. The R-white character of the Rosecomb bantam is therefore recessive to colour. The F_1 birds we hope to breed from in 1906.

(β) *Silkies.*—During the past summer a trio of Silkies was procured from Mr. Frank Rice, a well-known fancier. The ♂ and one of the ♀s. were each crossed with a Br. L. (Experiments 335 and 393). All the 10 offspring hatched out were coloured much like Br. L.'s, and there seems no doubt but that these Silkies resemble the R-white type. Here again birds have been reared in order to continue the experiments next year.

(γ) *Extracted R-Whites.*—We have among our records a set of experiments which were made with reference to comb characters, but which at the same time demonstrate indirectly the recessive nature of this type of white. In Experiment 93 (Rep. II, p. 100) a White Dorking of Creswell's strain was mated with an Indian game ♂. The occurrence of coloured birds from such a mating was at the time looked on with surprise, and they were considered as unexplained exceptions to the ordinary dominance of white (Rep. I, p. 141, note). Reasons have since been given for regarding this Wh. D. ♀ as a heterozygote of the two forms of white (Rep. II, p. 118 and p. 117 note). One of the coloured birds (♂ 904) resulting from this experiment was mated with a Br. L. ♀ (Experiment 164). From his breeding he must have been a heterozygote formed by a colour-bearing and an R-white gamete. Two of the coloured offspring resulting from this union were bred together (Experiment 253). Assuming they were each formed by the union of an R-white gamete from ♂ 904 and a colour-bearing gamete from the Br. L. ♀, we should look from such a mating for coloured and white offspring in the proportion of 3 : 1. Actually there were produced 46 coloured and 18 light chicks. One of these light birds (♂ 253) was reared, and in its adult plumage was pure white except for traces of pigment at the base of some of the tail feathers. In 1905 this bird was mated with 4 coloured hens (Experiments 345, 346). All the 95 chicks produced were without exception coloured. Many of these have been reared, and next year will form the basis of future experiments to elucidate the nature of the R-white.

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* Kindly given us by Mr. F. Slade.

1902. Experiment 93 .... ♂ I. G. × Wh. D. ♀
1903. Experiment 164 .... ♂ 904 (coloured) × Br. L. ♀
1904. Experiment 253 .... ♂ 834 (coloured) × 679 ♀
1905. Experiments 345 and 346... ♂ 253 (R—white) × 4 ♀ s. (all coloured)
95 coloured chicks.

Andalusians.—In Report I it was suggested that the blue colour of the Andalusian is probably* heterozygous, and in Report II (p. 118) figures were given in support of this view. During the past two years additional evidence has been acquired, and every form of mating has now been tested with the following results:—

No. of Experiment.	Nature of Mating.	Result.		
		Black.	Blue.	Wh. spl.
Rep. II, p. 118 ...	Blue ♀ s. × blue ♂	22	36	17
Exp. 276	Blue ♀ s. × blue ♂	19	42	22
(Total numbers for blue and blue		41	78	39)
Rep. II, p. 118 ...	Wh. spl. ♀ × Blue ♂	—	34	20
" " ...	Black ♀ × Blue ♂	19	27	—
Exp. 269	Wh. spl. ♀ s. × wh. spl. ♂ ...	—	—	40
" 270	Black ♀ × wh. spl. ♂	—	20	—
" 294	Black ♀ × black ♂	25	—	—

The colour of most of the chickens was determined in the down. In the blacks the down is black with the exception of the ventral surface, the tips of the wings, and sometimes parts of the head, which are white. The down in the blues is slaty-blue, similarly marked with white, whilst in the white splashed it is of an exceedingly pale blue tint as a rule, though sometimes practically colourless.

The above figures bear out the view we previously expressed as to the heterozygous nature of the blues, though before leaving this subject reference must be made to an apparently exceptional case. Among the young birds reared in Experiment 269 was one white ticked ♀. This bird behaved as if she were white × colour, whilst all Andalusians and their pure-bred offspring of all three sorts behave as coloured when crossed with coloured birds. The carriage and appearance of this bird was quite unlike that of the Andalusians. Moreover, her shanks were yellow. We have little hesitation in regarding her as the result of some accident.

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* This is true for other breeds also. Thus, we have found brown-striped down of Brown Leghorn dominant to the pale brown down of Malays (Experiments 330, 334, 361) and of Malay Bantams (Experiments 242, 283).

Brown-breasted Bantams.—We mentioned (Rep. II, p. 121) that we had received from Mrs. Staples-Browne a trio of bantams, F_1 from Brown-breasted × Black-red game. These birds were bred together in 1904, and the ♂ was bred with other hens in 1904 and 1905. The breeds concerned in these experiments are characterised by three forms of *down*-colour:—

	Down-colour.
Brown-breasted Game	Very dark brownish black.
Blk.-red Game	Brown striped.
Blk.-red Malay Bantam ...	Pale brown with some brownish buff on rump: quills showing dark.

Of these three forms of down-colour, brownish-black is dominant to both brown stripe and pale brown; heterozygous birds showing rather more brown, especially on the head. Brown stripe is dominant to pale brown.* The evidence for these statements appears in the following table:—

Composition of ♀.		Composition of ♂.	Result.		Expectation.	
			Br. blk.	Br. str.	Br. blk.	Br. str.
Exp. 267.	Br. blk. × br. str.	Br. blk. × br. str.	58	18	57	19
„ 268.	Pale br. × pale br.	„	7	6	6·5	6·5
„ 342.	Br. blk. × pale br.	„	16	7	17·25	5·75
„ 343.	Br. str. × pale br.	„	20	11	15·5	15·5

In Experiment 268, in addition, one exception occurred, viz., a pale brown chick. The origin of this exception was unexplained. We incline to regard it as due to some mistake.

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* This is true for other breeds also. Thus, we have found brown-striped down of Brown Leghorn dominant to the pale brown down of Malays (Experiments 339. 334, 361) and of Malay Bantams (Experiments 242, 283).

Explanation of Abbreviations used in Table.

W. L.	White Leghorn.
Br. L.	Brown Leghorn.
Buff L.	Buff Leghorn.
I. G.	Indian game.
G. B.	Game bantam.
Eg.	Egyptian.
O. E. G.	Old English game.
Wy.	Wyandotte.

W. And.	White splashed Andalusian.
B. And.	Blue Andalusian.
Bk. And.	Black Andalusian.
Mal.	Malay.
Mal. b.	Malay bantam.
Sil.	Silky.
W. R.	White Rosecomb.
B. R.	Black Rosecomb.

s.	single comb.
r.	rose comb.
p.	pea comb.
r.p.	rose-pea (= "walnut") comb.
r.s.	rose containing single.
p.s.	pea ,, ,,

int. p.	intermediate pea comb.
doub.	double comb.
slk.	"silky" comb.
e.	with extra toe.
n.e.	without extra toe.

The presence or absence of an extra toe has always been recorded, but in view of the irregularity of dominance mentioned in the last Report we have not attempted any further analysis of the behaviour of this character. All showing any indication of extra toe on both feet or on one only are recorded as e.t.

In the column giving the nature of the mating it has not been thought necessary to retain the complicated system of notation indicating ancestry which was used in the last Report. The breeding of any bird can, in each case, be ascertained from the pedigrees.

Table giving Details of Poultry Experiments (Combs and Feet).

1904.

Pen.	Exp. No.	Mother.	Origin (numbers refer to expts.).	Cb.	Ft.	Used in exp.	Father.	Origin (numbers refer to expts.).	Cb.	Ft.	Used in exp.	Nature of mating.	Combs.					Feet.	
													Offspring.					Offspring.	
													s.	r.	p.	r.p.	Dubious.	e.	No e.
1	196	463	W. L.	s.	no e.		Mal.		r.p.	n.e.		s. × r.p.			9	9			18
	197	839	90	,,	n.e.	200	,,		,,	,,		,,			8	6			14
	198	191	139	r.	,,		,,		,,	,,		r.s. × r.p.			6	20			26
	199	52	Mal.	r.p.	,,	389	,,		,,	,,		r.p. × r.p.				7			5
2	200	1 839	W. L. 90	s.	,,	197	256	172	r.	,,		r.s. × r.r.		27					27
3	201	843	190	r.p.	,,	232	806	190	r.p.	,,		r.p. × r.p.	2	5	7	16			31
	202	858	,,	,,	,,		,,	,,	,,	,,		,,	2	5	9	8			24
4	203	15	Mal.	,,	,,	288	689	152	,,	e.	303	,,			2	5		4	3
	204	682	152	,,	e.	212, 300	,,	,,	,,	,,	,,	,,	10	5	4	15		18	16
	205	530	,,	,,	,,		,,	,,	,,	,,	,,	,,	2	9	8	22		24	16
	206	701	,,	,,	,,		,,	,,	,,	,,	,,	,,	2	4	5	9		16	4
	207	664	I. G.	p.	n.e.		,,	,,	,,	,,	,,	p. × r.p.			5	7		3	8
	208	5 ♀ s.		s.	,,		,,	,,	,,	,,	,,	s. × r.p.	19	18	11	13		23	35
5	209	759	164	,,	,,		987	189	s.	n.e.		s. × s.	32						32
	210	323	166	,,	,,		,,	,,	,,	,,		,,	42						42
6	211	3 ♀ s.		,,	,,		457		,,	,,		,,	266						266
	212	682	152	r.p.	e.	204, 300	,,		,,	,,		r.p. × s.	4	5	2	4		3	13
	213	851	150	,,	n.e.	215	,,		,,	,,		,,	8	4	9	2			24
	214	425	167	,,	,,	238, 251	,,		,,	,,		,,	5	1		1			7

1904—*continued.*

Pen.	Exp. No.	Mother.	Origin (numbers refer to expts.).	Cb.	Ft.	Used in exp.	Father.	Origin (numbers refer to expts.).	Cb.	Ft.	Used in exp.	Nature of mating.	Combs. Offspring. s.	r.	p.	r.p.	Dubious.	Feet. Offspring. e.	No e.
7	215	765	150	r.p.	n.e.		909	189	r.p.	n.e.		r.p. × r.p.	4	19	19	33			75
	216	851	,,	,,	,,	213	,,	,,	,,	,,		,,	2	4	5	11			22
	217	546	W. L.	s.	,,		,,	,,	,,	,,		s. × r.p.	10	9	7	8			34
	218	312, 363		,,	,,		,,	,,	,,	,,		,,	21	27	24	21			93
8	219	446	143	doub.	,,		309		doub.	,,		doub. × doub.	6 *double.*					3	3
	220	342	,,	,,	,,		,,		,,			,,	14 ,,					4	9
	221	335	Eg.	,,	e.		,,		,,			,,	15 ,,					9	7
9	222	13	Buff L.	s.	n.e.		864	150	int. p.	n.e.		s. × int. p.	17 *int. p.* 46 *s.*						62
	223	726	172	int. p.	,,		,,	,,	,,	,,		int. p. × int. p.	28 *p. and int. p.* 7 *s.*						35
	224	782	Br. L.	s.	,,		,,	,,	,,	,,		s. × int. p.	9 *int. p.* 7 *s.*						16
	225	78	O. E. G.	,,	,,		,,	,,	,,	,,		,,	12 *int. p.* 18 *s.*						30
10	226	364		,,	,,		256	172	r.p.	,,		s. × r.p.	2		1	3			6
	227	895	W. L.	,,	,,	231	,,	,,	,,	,,		,,	3	4	5	5			17
11	228	912 690 921	190	p.	,,		919	190	p	,,		p.s. × p.s.	20		34				54
	229	79	111	,,	e.		,,	,,	,,	,,		,,	2		9			8	3
	230		Br. L.	s.	n.e.		,,	,,	,,	,,		s. × p.s.	2		3				5
	231	912	190	p.	,,	228	257		s.	,,		p.s. × s.	5		8				13
	232	843	190	r.p.	,,	201	,,		,,	,,		r.p. × s.	7	11	5	9			32
	233	13	Mal.	,,	,,	316	,,		,,	,,		,,		1		9			10
	234	701	152	,,	e.		,,		,,	,,		,,	1	1	4	6		6	6
12	235	146	157, *a*	s.	,,		116	157, *a*	,,	e.		s. × s.	31					30	1
	236	163	180	r.p.	n.e.	244	,,	,,	,,	,,		r.p. × s.	1	1		1		2	1

13	237	987	Br. L.	s.	n.e.		799	Br. L.	s.	n.e.	s. × s.	52					52
	238	425	167	r.p.	,,	214, 251	,,	,,	,,	,,	r.p. × s.	3	2	2			7
																	28
	239	12	Mal.	,,	,,		,,	,,	,,	,,	,,			16	12		
	240	887	172	,,	c.	255	,,	,,	,,	,,	,,	7	5	4	3	9	10
	241	269	180	,,	n.e.	254	,,	,,	,,	,,	,,	8	3	6	4		21
	242	54	Mal., *b*	,,	,,		,,	,,	,,	,,	,,				18		18
	243	386	185	,,	e.		,,	,,	,,	,,	,,	1	3	1	1	2	4
14	244	163	180	,,	n.e.	236	713	180	r.p.	,,	,,			2	2		4
	245	269	,,	,,	,,	241	,,	,,	,,	,,	,,	1	5	4	13		23
15	246	873	190	r.	,,		955	190	s.	,,	r.s. × s.	12	11				23
	247	326	174	s.	,,		,,	,,	,,	,,	s. × s.	33					33
	248	934	176	,,	,,		,,	,,	,,	,,	,,	37					37
	249	742	179	r.p.	,,		,,	,,	,,	,,	r.p. × s.	2	1	5	1		9
	250	26	Mal.	p.	,,		,,	,,	,,	,,	p. × s.			8			8
	251	425	167	r.p.	,,	214, 238	,,	,,	,,	,,	r.p. × s.		3	2			5
16	252	11	Buff L.	s.	,,		834	164	r.p.	,,	,,	18	13	15	14	19	40
	253	679	164	r.p.	,,		,,	,,	,,	,,	r.p. × r.p.	6	8	14	36	12	52
	254	269	180	,,	,,	241	,,	,,	,,	,,	,,	3	5	9	12	11	18
17	255	740 680 887 9	172 ,, ,, 162	,,	c.	271 278 240 272	283	172	,,	c.	,,				97	57	40
	256	2 ♀ s.		s.c.	n.e.		,,	,,	,,	,,	s. × r.p.				6	4	2
18	257	798	185	r.p.	,,	260	814		p.	n.e.	r.p. × p.			10	4		12
	258	743	,,	,,	,,	261	,,		,,	,,	,,			16	22		38
	259	386	,,	,,	e.	262	,,		,,	,,	,,			9	19	16	12
	260	798	,,	,,	n.e.	257	733		s.	,,	r.p. × s.	3	4	5	2		14
	261	743	,,	,,	,,	258	,,		,,	,,	,,	3	3	5	3		14
	262	386	,,	,,	e.	259	,,		,,	,,	,,	2	1	7	2	2	10
20	263	371	175	r.	n.e.		231		,,	,,	r.s. × s.	14	11				25
	264	674	167	,,	c.		,,		,,	,,	,,	16	21			17	20
	265	736		,,	n.e.		,,		,,	,,	,	21	22				43
	266	367	174	,,	,,		,,		,,	,,	,,	26	28				54
21	267	2 ♀ s.	G. B.	s.	,,		6	G. B.	,,	,,	s. × s.	76					76

1904—*continued.*

Pen.	Exp. No.	Mother.	Origin (numbers refer to expts.).	Cb.	Ft.	Used in exp.	Father.	Origin (numbers refer to expts.).	Cb.	Ft.	Used in exp.	Nature of mating.	Combs.					Feet.	
													Offspring.					Offspring.	
													s.	r.	p.	r.p.	Dubious.	e.	No e.
	268	55	Mal. B.	r.p.	n.e.		6	G. B.	s.	n.e.		r.p × s.				14			14
22	269	3 ♀ s.	W. And.	s.	,,		535	W. And.	,,	,,		s. × s.	49						49
	270	737	Bk. And.	,,	,,		,,	,,	,,	,,		,,	20						20
	271	740	172	r.p.	e.	255	,,	,,	,,	,,		r.p. × s.			8	3		3	8
	272	9	162	,,	,,	,,	,,	,,	,,	,,		,,	7	9	6	13		21	14
23	273	343	172	r.	e.		375	167	s.	,,		r. × s.		10				3	7
	274	319	,,	,,	,,		,,	,,	,,	,,		r.s. × s.	3	1				3	1
24	275	4 ♀ s.		s.	n e.		456	185	r.p.	,,		s. × r.p.	10	10	16	17			53
25	276	3 ♀ s.	B. And.	,,	,,		969	B.And.	s.	,,		s. × s.	86						86
	277	6	Mal.	r.p.	,,	334	,,	,,	,,	,,		r.p. × s.	2	1	1	1			5
	278	680	172	,,	e.	255	,,	,,	,,	,,		,,			10	11		7	12
26	279	2 ♀ s.	B. R.	r.	n.e.			B. R.	r.	,,		r. × r.		6					6
27	280	2 ♀ s.	W R.	,,	,,			W. R.	,,	,,		,,		65					65
28	281	3 ♀ s.	I. G.	p.	,,			I. G.	p.	,,		p. × p.			21				21
	282	264		s.	,,			,,	,,	,,		s. × p.			7				7
29	283	3 ♀ s.	Br. L.	,,	,,		53	Mal.B.	r.p.	,,		s. × r.p.		66		79			145
	284	54 55	Mal. B.	r.p.	,,	242, 268	,,	,,	,,	,,		r.p. × r.p.				19			18
	285	163	Eg.	doub.	,,		,,	,,	,,	,,		doub. × r.p.		4		13			17
	286	56		r.	e.	291	,,	,,	,,	,,		r. × r.p.		5		2		2	5
30	287	4 ♀ s.		s.	n.e.		9	Mal.	r.p.	,,		s. × r.p.			44	48			92
	288	15	Mal.	r.p.	,,	203	,,	,,	,,	,,		r.p. × r.p.			3	1			4
	289	11	,,	,,	,,		,,	,,	,,	,,		,,			3	5		1	7
31	290		W. R.	r.	,,			W. R.	r.	,,		r. × r.		26					26
	291	56		,,	e.	286		,,	,,	,,		,,		12				5	3
32	292	5 ♀ s.		s.	mixed		5	Mal.	p.	,,		s. × p.			76				

1905.

3	293	25	211	s.	n.e.		365	276	s.	n.e.		s. × s.	9						9
	294	410	276	,,	,,		,,	,,	,,	,,		,,	25						25
	295	316	W.L.	,,	,,		,,	,,	,,	,,		,,	17						17
	296	285	269	,,	,,		,,	,,	,,	,,		,,	8						8
	297	370	216	r.p.	,,		,,	,,	,,	,,		r.p. × s.		11		10			21
4	298	2 ♀ s.		s.	,,		593	239	r.p.	,,		s. × r.p.	13	10	17	10			50
6	299	3 ♀ s.		,,	,,		457		s.	n.e.		s. × s.	244						244
	300	682	152	r.p.	e.	204, 212	,,		,,	,,		r.p. × s.	3	4	2	3		3	8
	301	765	Mal.	p.	n.e.		,,		,,	,,		p. × s.			23				23
	302	231	202	r.p.	,,		,,		,,	,,		r.p. × s.	4	4	2	2			12
8	303	3 ♀ s.	W. L.	s.	,,		689	152	r.p.	e.	203–8	s. × r.p.	2	5	4	3		5	10
	304	665	Mal.	p.	,,		,,	,,	,,	,,	,,	p. × r.p.			3	1		2	2
10	305	3 ♀ s.		s.	,,		389	203	,,	,,		s. × r.p.			14	22	3	17	21
11	306	3 ♀ s.		,,	,,		23	218	,,	n.e.		,,	17	17	10	6			50
12	307	109	180	r.p.	,,		26	211	s.	,,		r.p. × s.	14	23	22	21			80
	308	58	259	,,	e.		,,	,,	,,	,,		,,	2		3	4		2	7
	309	539	239	,,	n.e.	319	,,	,,	,,	,,		,,	6	7	9	6			28
	310	466	197	,,	,,		,,	,,	,,	,,		,,	5	6	3	7			21
	311	486	283	,,	,,		,,	,,	,,	,,		,,	5	8	6	7			27
	312	601	252	,,	e.		,,	,,	,,	,,		,,		5	3	5		6	7
13	313	2 ♀ s.		s.	n.e.		559	283	r.p.	,,		s. × r.p.	11	7	8	9			35
14	314	3 ♀ s.		,,	,,		360	216	,,	,,		,,			18	19	5		43
15	315	12	253	r.p.	,,		37	211	s.	,,		r.p. × s.		3	1	3			7
	316	13	Mal.	,,	,,	233	,,	,,	,,	,,		,,		8		2			10
	317	53	259	,,	e.		,,	,,	,,	,,		,,	3	6	2	4		7	8
	318	36	218	,,	n.e.		,,	,,	,,	,,		,,	4	2	6	5			17
	319	539	239	,,	,,	309	,,	,,	,,	,,		,,				1			1
	320	474	283	,,	,,	326	,,	,,	,,	,,		,,	11	8	7	2			28
	321	767	Mal.	p.	,,		,,	,,	,,	,,		p. × s.			3				3
	322	766	,,	r.p.	,,		,,	,,	,,	,,		r.p. × s.			2				2
	323	414	217	,,	,,	361, 364	,,	,,	,,	,,		,,		2	2				4
	324	495	239	,,	,,		,,	,,	,,	,,		,,	9	10	15	14			49

1905—*continued.*

Pen.	Exp. No.	Mother.	Origin (numbers refer to expts.).	Cb.	Ft.	Used in exp.	Father.	Origin (numbers refer to expts.).	Cb.	Ft.	Used in exp.	Nature of mating.	Combs. Offspring. s.	r.	p.	r.p.	Dubious.	Feet. Offspring. e.	No e.
	325	209	258	r.p.	n.e.		37	211	s.	n.e.		r.p. × s.	2	3		3			8
16	326	474	239	,,	,,	320	432	Br. L.	,,	,,		,,	1	2	3	3			9
	327	488	,,	,,	,,		,,	,,	,,	,,		,,	10	12	11	11			44
	328	162	258	,,	,,		,,	,,	,,	,,		,,			15	8			23
	329	577	239	,,	,,		,,	,,	,,	,,		,,	2	2	4	4			12
	330	582	232	r.	,,		,,	,,	,,	,,		r.s. × s.	9	7					16
	331	151	258	r.p.	,,		,,	,,	,,	,,		r.p. × s.	4	2	6	2			14
	332	324	236	,,	c.		,,	,,	,,	,,		,,		2	1	1		1	3
	333	208	206	,,	n.e.		,,	,,	,,	,,		,,				14			14
	334	6	Mal.	,,	,,	277	,,	,,	,,	,,		,,	7	2	2	3			15
	335	349	Sil.	slk.	e.		,,	,,	,,	,,		slk. × s.		8 *silk.*				5	2
17	336	3 ♀ s.		s.	n.e.		421	216	r.p.	,,		s. × r.p.			58	52			108
	337	600	215	r.p.	,,		,,	,,	,,	,,		r.p. × r.p.			20	44			64
18	338	264		s.	,,		415	204	,,	,,		s. × r.p.		21		20			41
	339	452	276	,,	,,	346	,,	,,	,,	,,		,,		6		10			16
20	340	49	222	,,	,,		56	222	int.p.	,,		s. × int.p.	38 + 28 *int. p.*				3		69
	341	2 ♀ s.	Wy.	r.	,,		,,	,,	,,	,,		r. × int.p.		4					4
21	342	{ 623, 632 }	268	r.p.	,,		6	G. B.	s.	,,		r.p. × s.	8	7	3	5			23
	343	649	268	,,	,,		,,	,,	,,	,,		,,	4	11	5	10			30
	344	532	285	,,	,,		,,	,,	,,	,,		,,	4	2	4	3			13
22	345	3 ♀ s.		s.	,,		144	253	r.p.	,,		s. × r.p.	14	24	19	17			74
	346	452	276	,,	,,	339	,,	,,	,,	,,		,,	4	2	7	8			21
	347	895	W. L.	,,	,,		,,	,,	,,	,,		,,	6	1	8	1			15
	348	315	,,	,,	,,		,,	,,	,,	,,		,,	11	1	9	2			23

25	349	3 ♀ s.	211	s.	n.c.		116	258	r.p.	n.e.		s. × r.p.	16	9	14	4			43
26	350	4 ♀ s.	W. R.	r.	,,		760	B. R.	r.	,,	356	r. × r.		55					58
30	351	357	Br. L.	s.	,,			Mal.	r.p.	,,		s. × r.p.				28			28
	352	667	Mal.	r.p.	,,			,,	,,	,,		r.p. × r.p.				4			4
	353	682	,,	,,	,,	385		,,	,,	,,		,,				9			9
	354	681	,,	,,	,,			,,	,,	,,		,,				5			5
32	355	2 ♀ s.		s.	,,		192	258	,,	,,		s. × r.p.			26	33	2		61
33	356	,,	W. R.	r.	,,		760	B. R.	r.	,,	350	r. × r.		24					24
34	357	424	230	s.	,,		184	258	r.p.	,,		s. × r.p.			3	13			16
	358	603	211	,,	,,		,,	,,	,,	,,		,,			16	11			27
35	359	537	239	r.p.	,,		384	Br. L.	s.	,,		r.p. × s.	6	3	5	4			18
	360	379	215	,,	,,		,,	,,	,,	,,		,,		9		4			13
	361	414	217	,,	,,	323, 364	,,	,,	,,	,,		,,	7	3	1	2			13
36	362	2 ♀ s.		s.	,,		292	216	r.p.	,,		s. × r.p.	8	6	8	10			32
37	363	502	283	r.p.	,,		482	Br. L.	s.	,,		r.p. × s.	10	4	3	6			24
	364	414	217	,,	,,	323, 361	,,	,,	,,	,,		,,	2	1		5			8
	365	643	242	,,	,,		,,	,,	,,	,,		,,	5	4	5	3			16
	366	418	215	,,	,,		,,	,,	,,	,,		,,				9			7
	367	404	Br. L.	s.	,,	393	,,	,,	,,	,,		s. × s.	32						32
38	368	505	224	,,	,,	387		I. G.	p.	,,		s. × p.	6		5				11
39	369	2 ♀ s.	B. R.	r.	,,		585	W. R.	r.	,,		r. × r.		7					7
	370	659	267	s.	,,		,,	,,	,,	,,		s. × r.		6					6
40	371	289	269	,,	,,		257	202	r.p.	,,		s. × r.p.		8		6			14
	372	515	Br. L.	,,	,,		,,	,,	,,	,,		,,		10		9			18
41	373	2 ♀ s.	211	,,	,,		549	233	,,	,,		,,	39	27	36	16			118
	374	4 ♀ s.	Br. L.	,,	,,		,,	,,	,,	,,		,,	17	20	19	12			68
42	375	285	269	,,	,,		W. And.	269	s.	,,		s. × s.	16						16
	376	227	,,	,,	,,		,,	,,	,,	,,		,,	16						16
	377	317	W. L.	,,	,,		,,	,,	,,	,,		,,	36						36
43	378	2 ♀ s.	211	,,	,,			Mal.	p.	,,		s. × p.	31						31
44	379	435	Eg.	doub.	,,		431	Eg.	doub.	e.		doub. × doub.		11 *doub.*				6	5
	380	2 ♀ s.		s.	,,		,,	,,	,,	,,		s. × doub.		7 *doub.*				7	
	381		Wy.	r.	,,		,,	,,	,,	,,		r. × doub.		9				8	1
45	382	2 ♀ s.	211	s.	,,		467	283	r.p.	n.e.		s. × r.p.	13	10	15	10			48

1905—*continued.*

Pen.	Exp. No.	Mother.	Origin (numbers refer to expts.).	Cb.	Ft.	Used in exp.	Father.	Origin (numbers refer to expts.).	Cb.	Ft.	Used in exp.	Nature of mating.	Combs. Offspring. s.	r.	p.	r.p.	Dubious.	Feet. Offspring. e.	No e.
46	383	295	206	r.p.	e.		133	211	s.	n.e.		s. × r.p.				11		10	1
	384	665	Mal.	p.	n.e.		,,	,,	,,	,,		s. × p.			10				10
	385	682	,,	r.p.	,,	353	,,	,,	,,	,,		s. × r.p.			10	5			15
	386	578	233	,,	,,		,,	,,	,,	,,		,,		1	2	4			7
47	387	505	224	s.	,,	368	183	258	r.p.	,,		s. × r.p.			5	2			7
	388	1		,,	,,		,,	,,	,,	,,		,,			4	6			10
	389	52	Mal.	r.p.	,,	199	,,	,,	,,	,,		r.p. × r.p.				3			3
48	390	2 ♀ s.	Br. L.	s.	,,		198	260	,,	,,		s. × r.p.			11	12			23
49	391	2 ♀ s.	211	,,	,,		57	258	,,	,,		,,			18	10			28
51	392	350	Sil.	silk	e.		348	Sil.	silk	e.		silk. × silk	8 *silk.*					7	1
	393	404	Br. L.	s.	n.e.	367	,,	,,	,,	,,		s. × silk.	2 *silk.*					2	

SWEET PEAS (*Lathyrus odoratus*).

(Experiments by W. Bateson, E. R. Saunders, and R. C. Punnett.)

Sweet Peas.

Among the various crosses mentioned in our last report as having reached the F_2 stage was that of Emily Henderson with long pollen (E. H. l.) × Emily Henderson with round pollen (E. H. rd). The F_1 plant resulting from these 2 strains of whites is always coloured and is almost always purple. In the F_2 generation from the purple F_1 appear 3 main colour classes, viz.,[*] blues, reds, and whites. The blues may be subdivided into (1) purples with blue wings, *i.e.*, "Purple Invincible" (P. I.); (2) purples with purple wings (P.p.w.); and (3) Picotees (Pic.). Similarly the reds may be classed as (1) reds with pale pink wings, *i.e.*, "Painted Lady", (P. L.); (2) reds with red wings, *i.e.*, "Miss Hunt" (M. H.); and (3) tinged whites (T. W.). Further, any plant may have long or round pollen, and any coloured plant may exhibit either a dark or a light axil. The work of the past two years has been chiefly concerned with the results of this original cross, and it is now apparent that we are dealing with 7 pairs of allelomorphic characters. These are—

Dominant.		Recessive.	
[†]1st colour factor	(C).	Absence of 1st colour factor	(c).
2nd ,, ,, ...	(R).	,, 2nd ,,	(r).
Blueness	(B).	,, blueness	(b).
Light wing	(wl).	Dark wing	(wd).
Uniform colour distribution	(D).	Colour on edge only	(E).
Long pollen	(L.).	Round pollen......................	(rd.).
Dark axil.		Light axil.	

Blues, Reds, and Whites.—For the present we may confine our attention to the first three of these allelomorphic pairs. As the scheme shows, the manifestation of colour depends upon the simultaneous presence of C and R in the zygote. Any plant homozygous for either c or r, or for both, must be white. Whether a coloured plant belongs to the blue or to the red class depends upon the presence or absence of B in the zygote, but the blue character can only show itself in such zygotes as contain both C and R.

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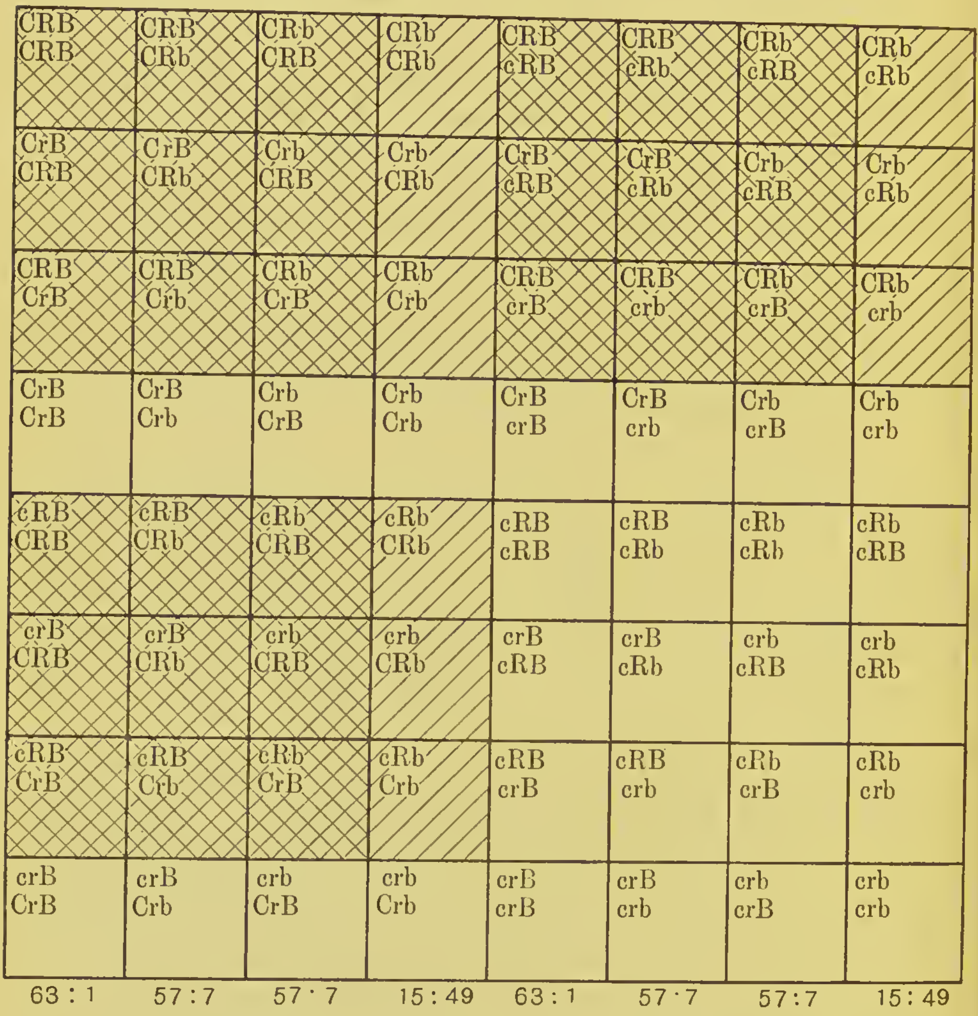
[*] There are apparently but two classes of sap-coloured Sweet Peas, viz., blues and reds. The blues resulting from the E. H. cross are all purple in shade, but, bearing in mind the existence of various tints in other strains, we prefer to make use here of the more comprehensive term.

[†] The behaviour of these two factors strongly suggests that one of them (C) may be a colour-forming stuff which gives rise to colour when acted upon by the other factor (R). We should then have to regard this latter as of the nature of an enzyme, but, in the absence of direct chemical evidence, we consider it advisable to use non-committal terms for the present.

We consider the pure E. H. long strain used to be homozygous for C, r, and B, and the pure E. H. rd. strain to be homozygous for c, R, and b. Consequently the zygote formed by the cross E. H. l × E. H. rd. must be of the constitution Cc.Rr.Bb. And such an F$_1$ zygote gives rise in gametogenesis to equal numbers of 8 kinds of gametes, viz., CRB, CRb, CrB, Crb, cRB, cRb, crB, crb. The various zygotes formed by these gametes when the F$_1$ plant is selfed are shown in the accompanying figure (fig. 2).



▨ CRB CRB	▨ CRB CRb	▨ CRb CRB	▧ CRb CRb	▨ CRB cRB	▨ CRB cRb	▨ CRb cRB	▧ CRb cRb
▨ CrB CRB	▨ CrB CRb	▨ Crb CRB	▧ Crb CRb	▨ CrB cRB	▨ CrB cRb	▨ Crb cRB	▧ Crb cRb
▨ CRB CrB	▨ CRB Crb	▨ CRb CrB	▧ CRb Crb	▨ CRB crB	▨ CRB crb	▨ CRb crB	▧ CRb crb
CrB CrB	CrB Crb	Crb CrB	Crb Crb	CrB crB	CrB crb	Crb crB	Crb crb
▨ cRB CRB	▨ cRB CRb	▨ cRb CRB	▧ cRb CRb	cRB cRB	cRB cRb	cRb cRb	cRb cRB
▨ crB CRB	▨ crB CRb	▨ crb CRB	▧ crb CRb	crB cRB	crB cRb	crb cRB	crb cRb
▨ cRB CrB	▨ cRB Crb	▨ cRb CrB	▧ cRb Crb	cRB crB	cRB crb	cRb crB	cRb crb
crB CrB	crB Crb	crb CrB	crb Crb	crB crB	crB crb	crb crB	crb crb
63 : 1	57 : 7	57 · 7	15 : 49	63 : 1	57 · 7	57 : 7	15 : 49

Fig. 2.—Scheme of distribution of colour-factors in F$_2$. From E. Henderson (Sweet Pea), white, long pollen × white, round.

The table is an expansion of that shown in fig. 1, and exhibits the effect of the blue factor, B. The cross-hatched squares are purple-flowered plants; the single-hatched are red; the plain are whites.

The figures at the foot of each column show the ratio of long-pollened to round-pollened in each square of that column, on the hypothesis given in the text.

In 36 of the 64 zygotes so formed both R and C are present, and these zygotes consequently develop into coloured plants. The remaining 28 give rise to whites, and the ratio of coloured to white is therefore 9 : 7. Of the 36 coloured 27 are either homozygous or heterozygous for B and consequently are blue, the remaining 9 being reds. Hence we expect in F_2 blues, reds, and whites in the proportion 27 : 9 : 28. Actually experiment* has so far given 1,634 blues, 498 reds, and 1,593 whites out of a total of 3,725 F_2 plants (*cf.* Table, p. 37) where theory would demand 1,571 blues, 524 reds, and 1,630 whites. Bearing in mind the fact that all these plants were left to nature and that *Megachile* was often at work (*cf.* Rep. II, p. 95), a slight excess of blues is what we should expect, for vicinism (de Vries) might result in the production of a blue plant from a non-blue ♀ gamete, but would never prevent a blue ♀ gamete from giving rise to a blue plant.

Picotees and Tinged Whites.—In families where picotees and tinged whites occur these types behave as recessives to the corresponding fully coloured purples and reds. The tinged whites bear to the reds the same relation that the picotees do to the purples. The 4 classes pur., pic., red, and T. W. appear in F_2 in the ratio 9 : 3 : 3 : 1. The actual numbers (Table, p. 37) are 819 pur., 259 pic., 252 red, and 68 T. W., where expectation is 780, 260, 260, and 86 respectively. The slight deficiency of T. W., the ultimate recessive among the colours, and the small excess of the dominant purple is to be expected when the vicinism due to *Megachile* is borne in mind. It may be added that the recessive nature of Pic. and T. W. to purple and red respectively has been confirmed by the behaviour of the F_3 generation.

Light Wings and Dark Wings.—In some F_2 families 2 sorts of

DD wl.wl. (P.I.)	DD wl.wd. (P.I.)	DE wl.wl. (P.I.)	DE wl.wd. (P.I.)
DD wl.wd. (P.I.)	DD wd.wd. (P.p.w.)	DE wl.wd. (P.I.)	DE wd.wd. (P.p.w.)
DE wl.wl. (P.I.)	DE wl.wd. (P.I.)	EE wl.wl (Pic.)	EE wl.wd. (Pic.)
DE wl.wd. (P.I.)	DE wd.wd. (P.p.w)	EE wl.wd. (Pic.)	EE wd.wd. (Pic.)

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* These figures include families where Blanche Burpee (white) was used as the long parent in place of E. H. long. In such cases there appears to be no difference in the distribution of the characters under consideration as compared with the cross E. H. long × E. H. rd.

purples and reds can be distinguished. The purples may have purple standards and blue wings (Purple Invincible), or they may have deep purple wings (P.p.w.). Similarly among the reds the wings may be pale as in Painted Lady, or red as in Miss Hunt. These differences were not always regarded in F_2 plants, but subsequent breeding of F_3 plants from F_2 individuals showed that* dark wings (P.p.w. or M. H.) are recessive to light wings (P. I. or P. L.). Thus from the seed of an F_2 pur. lt. ax. long were grown F_3 plants in 1904, of which 24 were P. I., 12 were P.p.w., and 11 were Pic., a fairly close approximation to the expected ratio 9 : 3 : 4. We regard the F_2 plant as having been heterozygous for both D and wl, and therefore of the constitution DE.wl.wd. Consequently its gametes were Dwl, Dwd, Ewl, and Ewd, and the number and constitution of the zygotes produced by such gametes is shown in the accompanying table. In 1905 a further generation was raised from many of these F_3 plants. The results obtained are set forth below—

F_3 parent.	Constitution of F_3 parent.	F_4 generation.			Expectation.		
		P.I.	Ppw.	Pic.	P.I.	Ppw.	Pic.
P.I. (1 plant) ...	Dwl. Dwl.	all	—	—	all	—	—
P.I. (3 plants)...	Dwl. Ewl.	70	—	31	76	—	25
P.I.	Dwl. Dwd.	(not met with)					
P.I. (4 plants)...	Dwl. Ewd.	103	32	42	100	33	44
Ppw. (4 plants)	Dwd. Dwd.	—	all	—	—	all	—
Ppw. (3 ,,	Dwd. Ewd.	—	86	36	—	92	30
Pic. (5 ,,	Ewl. Ewl. or Ewl. Ewd. or Ewd. Ewd.	—	—	all	—	—	all

A number of crosses made between various F_4 individuals gave results which further illustrate the working of the scheme. Certain of these crosses also demonstrated the existence of different kinds of Pics. Thus 1 Pic. on being crossed with a homozygous p.p.w. gave 5 P.p.w. only, and was, therefore, in all probability of the constitution Ewd.Ewd. Another Pic. similarly crossed gave 2 P. I.s, thus proving that the light wing factor (wl) must have been present in this instance.

Pollen.—The character round pollen we have shown to be recessive to long pollen. Of the 3,725 F_2 plants (Table, p. 37), 2,844 were long and 881 were round, a ratio of 3·23 : 1. Here, again, vicinism would account for the slight excess of longs. In our last Report (p. 89) we pointed out that whilst the ratio 3 : 1 appears to hold good for the whites, the blues show a great excess of longs and the reds of rounds. The more recent results are in accordance with the earlier ones, and the total numbers now available are as follows :—

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* We have not regarded these distinctions in the case of the picotees and tinged whites.

	Long.	Round.	*Ratio.*
Blue	1528	106	*14·41 : 1*
Red	117	381	*1 : 3·25*
White	1199	394	*3·04 : 1*
	2844	881	*3·23 : 1*

These proportions are quite definite throughout the different families, and indicate some form of gametic coupling between the blue and long and between the red and round factors (*cf.* p. 9). We hope to give a full account of this phenomenon when the experiments now in progress are completed.

In families where picotees and tinged whites are present, the proportion of rounds is lower among the purples but higher among the picotees, though, as the table below shows, the proportion of longs is not very different in the reds and tinged whites :—

	Long.	Round.	*Ratio.*
Purple...............	777	42	*18·5 : 1*
Picotee	235	24	*9·8 : 1*
Red	60	192	*1 : 3·2*
Tinged white	18	50	*1 : 2·8*

The system most nearly fitting the observed figures is that mentioned in the Introduction (p. 9). On that hypothesis, of 16 gametes 7 bear B (blue factor) with long pollen ; 1 bears B with round pollen ; 7 bear *b* (absence of blue) with round pollen ; 1 bears *b* with long pollen. The ratio of long to round would then be

In the blue	11·8 : 1
,, red	1 : 3·2$\dot{6}$
,, white	3 : 1
,, whole F_2 generation	3 : 1

The following figures show the closeness with which this system corresponds with observation :—

	Purple.		Red.		White.	
	Long.	Round.	Long.	Round.	Long.	Round
Observed	1528	106	117	381	1199	394
Calculated	1448·5	122·7	122·7	401·5	1220·5	407·4

There are, however, reasons for anticipating that other specific complications in the system of coupling will be disclosed when a further analysis is made, based upon the other characters.

Axil.—Of the 2132 coloured plants 1587 had dark and 545 had light axils, giving a ratio of 2·92 : 1. One would have expected vicinism to have led to a slight excess of dark axils. That the balance is a trifle the other way is probably due to the fact that the axils are sometimes difficult to distingish when the plants are not recorded before they are somewhat past their prime. In such cases the axils fade, and some dk. ax. plants might be recorded as lt. ax., though the reverse could not occur. On the other hand, one must not overlook the possibility that there may be some coupling of dk. ax. with absence of C and R. That the axil character may be concerned in the phenomenon of gametic coupling is shown by its behaviour in families where picotees and tinged whites occur. The following figures, which have been brought together from such families, point to a distinct coupling of lt. ax. with red :—

	Dk. ax.	Lt. ax.	*Ratio.*
Blues	818	260	*3·15 : 1*
Reds	204	116	*1·76 : 1*

We hope that the experiments now in progress will throw further light on this interesting phenomenon.

Details of F_2 from white, long pollen × ditto round pollen and reciprocal, F_1 being purple.

	Reference number.	Pur.				Pic.				Red.				T.W.				White.	
		dk.		lt.		dk.		lt.		dk.		lt.		dk.		lt.			
		l.	r.	l.	r.	l.	r.	l.	r.	l.	r.	l.	r.	l.	r.	l.	r.	l.	r.
With Pic. and T.W.	Report II, p. 89	176	11	45	2	39	7	15	1	10	23	6	17	2	5	3	7	195	73
	1904, No. 81	81	3	29	0	29	0	3	0	7	16	6	6	2	7	1	2	104	32
	1905 ,, 250	87	7	30	1	25	1	12	3	10	20	3	16	2	4	1	4	125	40
	,, ,, 251	15	1	4	1	7	0	0	0	0	8	1	0	0	0	0	0	19	6
	,, ,, 252	102	3	44	1	44	5	9	1	4	24	4	13	4	7	1	1	182	69
	,, ,, 254	23	1	6	1	7	1	1	0	1	3	1	1	0	1	0	1	30	4
	,, ,, 308	97	8	38	2	33	5	11	0	6	31	1	14	0	7	2	4	141	46
		819 [*780*]				259 [*260*]				252 [*260*]				68 [*86*]				1066 [*1078*]	
Without Pic. and T.W.	1904, No. 71	23	6	10	0					0	6	0	4					39	9
	,, ,, 72	36	3	9	0					4	11	0	1					27	7
	,, ,, 73	60	6	18	2					5	18	0	4					44	19
	,, ,, 74	39	1	18	1					2	9	3	2					38	15
	1905 ,, 253*	32	2	5	0					3	6	0	4					42	16
	,, ,, 309*	59	2	11	4					8	17	4	4					63	15
	,, ,, 310*	125	6	29	3					5	29	3	12					116	36
	,, ,, 311*	30	3	12	1					2	7	0	5					34	7
		556 [*532*]								178 [*177*]								527 [*552*]	
	Total	Blue ... 1634 [*1571*]								Red ... 498 [*524*]								White... 1593 [*1630*]	

* Original cross E. H., round × Blanche Burpee, long: hoods appear in F_2.

STOCKS.

(Experiments by E. R. SAUNDERS.)

Flower-Colour and Hoariness.

The general scheme underlying the complications witnessed in the case of Stocks is now clear, and an outline of it is given in the Introduction. As stated (Rep. II, p. 8), though any two sap-coloured glabrous strains of Ten-Week Stocks give glabrous F_1, yet the mating of white with cream or of either with a sap-coloured variety, results in hoary F_1. The distribution of the characters, sap-colour and hoariness, in F_2 shows (1) that the colour is due to the combination of two independent factors which we shall call C and R, each of which is allelomorphic to *c* and *r* respectively—absence of the same factors.

(2) That the hoariness is similarly due to the combination of another pair of factors H and K allelomorphic to *h* and *k*—absence of each respectively.

(3) That the hoariness due to presence of H and K is not manifested unless C and R are also both present.

In F_2 from *cream glabrous × white glabrous* all the hoary are sap-coloured and all the glabrous are white or cream (*i.e.*, non-sap-coloured), though in F_2 from white or cream × sap-coloured, there are coloured glabrous as well as uncoloured glabrous and coloured hoary plants. The two classes, sap-coloured hoary and non-sap-coloured glabrous, are in the ratio 9 : 7. Therefore the cream and the white parents both carry H and K, though, being without sap-colour, they are glabrous.*

In F_2 from *white (or cream) glabrous × sap-coloured glabrous* there are 3 coloured : 1 white, but again the hoary to glabrous are 9 : 7. Therefore the sap-coloured type contains one of the components of hoariness, say H. The allelomorphic composition of the three kinds of glabrous plants may be represented thus :—

White	CrHK.
Cream	cRHK.
Sap-colours	CRHk.

The assignment of C and R is of course arbitrary, for all that can be declared is that one is present in cream and one in white. Similarly it may be either H or K which is absent in the sap-coloured types.

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* Otherwise, if cream contained one factor (H) and white the other (K), or if one type (say cream) contained both factors, and the other (white) neither, some of the F_2 plants should be glabrous and sap-coloured, since some gametic unions would yield zygotes containing CRHk or CRhK. But this, as stated above, is not the case.

The combinations of characters exhibited in F_2 is graphically shown in the diagrams. The squares represent zygotes. The hoary are indicated with shading (partial or complete), the coloured similarly with blue. Each undivided square represents a homozygote yielding an unmixed F_3 similar in character to itself. In a subdivided square the several combinations of colour and shading indicate the (qualitatively, not quantitatively) different F_3 forms derivable from that particular zygote.

In this discussion the sap-coloured plants have been dealt with as a whole. As a matter of fact they consist (as stated in the Introduction) of two main classes, purples due to the presence of a factor B, and reds in which the same factor is absent (*b*). Each of these two classes may be again divided into subordinate groups, purple and plum on the one hand, red and copper on the other; and the evidence clearly shows that the subdivision of each class is simply due to the superposed distribution of another factor which may be present or absent, determining the quality of the colour in the respective classes.* The factor which determines the appearance of the subordinate colour forms is evidently introduced by the white, for these modified colours occurred in F_2 from white × red, but not in F_2 from cream × red (Rep. II, p. 27).

These four sap-colours are all that appear in F_2 from white × cream, but the *pale* colours, flesh and pale purple, for example, characteristic of other strains, would need a separate analysis to exhibit their interrelations.

In the diagrams no account is taken of the distinction between white and cream. As previously stated, cream, that is, yellow plastid colour, is recessive to white or uncoloured plastids, and it might be expected that this plastid-character was merely superposed on the others; but a large and unexplained deficiency of creams noticed in several cases indicates a distinct complication. How far this deficiency is attributable to the late-flowering habit of the cream forms is at present undetermined.

The factors determining colour and surface-character being thus interrelated, it is evident that the nature of only a small proportion of the numerous types of individuals composing F_2 will be recognisable by inspection alone. In the case of white glabrous × cream glabrous only 10 distinct forms can be distinguished in this generation without further breeding, viz., 2 (white and cream) among the glabrous, and 8 (4 self sap-colours and the corresponding bicolours) among the hoary plants. But the recombinations of the several factors discussed above yield 243 distinct types in F$_2$, requiring 1024 (4^5) individuals to exhibit them all in their relative proportions. On setting out the possible combinations, 108 of these types will be found to occur among hoary, 135 among glabrous individuals. In the case of the hoary plants much can be learnt from the results of *self*-fertilisation; thus 54 F$_2$ types can be distinguished if the analysis of the F$_3$ families, thus produced, is merely qualitative, 81 if the quantitative composition is also known. The whole 108, however, can only be identified if the self-fertilisation is supplemented by suitable cross-breeding, since by this method only, as yet, are we able to distinguish between two otherwise similar individuals, one being homozygous as regards C and heterozygous as regards R and the other heterozygous as to C and homozygous as to R (*cf.* sqs. 3 and 9 with sqs. 7 and 10, fig. 3). In the glabrous plants, on the other hand, constitutional differences other than those affecting plastid colour can only be detected by *cross*-breeding. Table II shows

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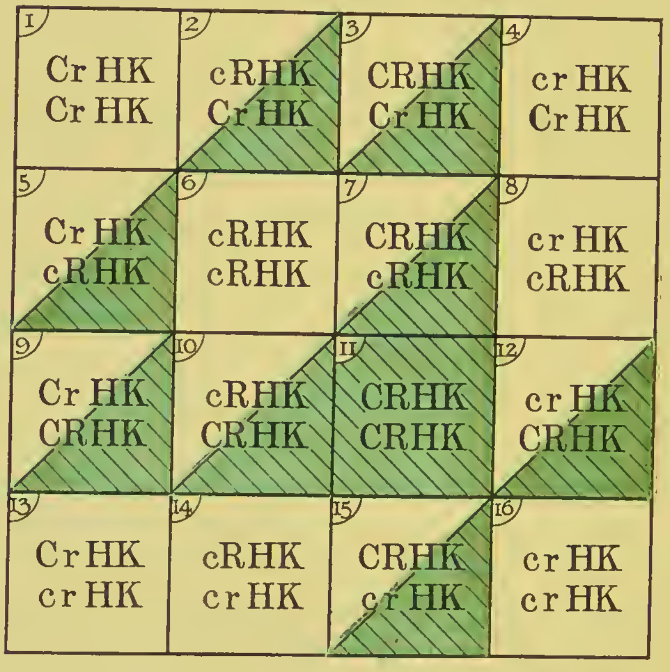
* The relations existing between the four sap-colours, purple, plum, red, and copper, appear to be similar to those observed by Tschermak in the case of the *reinviolett*, *aschviolett*, *reinrosa*, and *aschrosa*, resulting in F_2, from a cross between a blood-red hoary and a white glabrous, if, indeed, the two series of colours are not identical. 'Beihefte z. Bot. Centralb.,' Bd. 16, Heft 1, 1903.

FIG. 3.—F$_2$ from White glabrous × Cream glabrous.

Ratio of hoary to glabrous ...... 9 : 7.
,, coloured to white ...... 9 : 7.



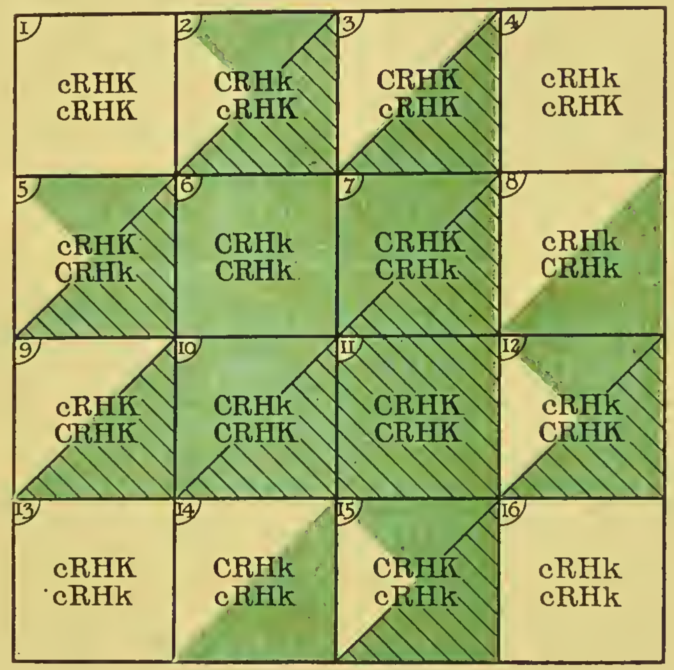
1 Cr HK Cr HK	2 cRHK Cr HK	3 CRHK Cr HK	4 cr HK Cr HK
5 Cr HK cRHK	6 cRHK cRHK	7 CRHK cRHK	8 cr HK cRHK
9 Cr HK CRHK	10 cRHK CRHK	11 CRHK CRHK	12 cr HK CRHK
13 Cr HK cr HK	14 cRHK cr HK	15 CRHK cr HK	16 cr HK cr HK

Each square is a zygote. When C meets R there is sap-colour in the flower (indicated by blue), and though H and K are present in all, the coloured alone are hoary (indicated by hatching). The undivided squares represent homozygotes with uniform offspring. The subdivision of a square shows that the zygote it represents will give a mixed offspring, but no attempt is made to show the *proportions* in which the various forms will occur in F$_3$.

the 54 qualitatively different types of hoary individuals which will occur in F_2, and their distribution among the 8 recognisably distinct forms appearing in that generation. The evidence already available plainly indicates that if the experiment were carried out upon a sufficiently large scale the full number of types would be obtained. Briefly summarised the facts were as follows: Fifty-seven hoary F_2 plants were tested by self-fertilisation. In the case of 15 the results were inconclusive owing to the small number of offspring obtained; the remaining 42 were found to correspond with 18 of the 54 qualitatively different types shown in Table II. [These types are marked in the table with an asterisk.] A full analysis of the F_3 families is given in Table III.

FIG. 4.—F_2 from Cream Glabrous × Sap-coloured Glabrous.

Ratio of hoary to glabrous .... 9 : 7
" coloured to white .... 3 : 1



Hatching indicates hoariness. Blue shows sap-colour in the flower. Homozygous plants with uniform offspring are indicated by undivided squares. Squares representing heterozygotes are subdivided, and the distribution of colour and hatching in them shows the nature of the mixture to be found in their progeny (F_3), but no attempt is made to show the *proportions* in which the various forms will occur.

Certain other corollaries which follow from this account of the gametic composition of the F_2 plants can be tested by the F_3 generation, and these also may be considered in the particular case of white glabrous × cream glabrous (CrBHK × cRbHK).

Expectation (see Argument p. 38 and fig. 3, p. 40).	Results Observed (see Detailed Analysis, Table III, p. 49, and Table IV, p. 52).
1. That some of the hoary F_2 plants will be *heterozygous* in regard to *both* C and R, giving a mixed offspring in the proportion of 9H : 7G.	Fourteen hoary F_2 plants gave a mixture of hoary and glabrous in proportions varying between 9 : 7·9 and 9 : 5·9, *the average ratio being exactly 9H : 7G.*
2. That others will be *heterozygous* only as regards *either* C *or* R, and will yield a mixture in the ratio of 3H : 1G.	Twenty-two hoary F_2 plants gave a mixture of hoary and glabrous in proportions varying between 3 : 1·3 and 3 : 0·7; *the average ratio being exactly 3H : 1G.*
3. That others will be *homozygous* as regards C and R, and will yield only hoary offspring.	Five hoary F_2 plants yielded together 704 offspring, *all hoary.*
4. That the numbers of these three kinds of individuals will be in the ratio of 4 : 4 : 1.	The numbers of the three kinds of individuals obtained from 41 plants taken at random were 14, 22, and 5 respectively, where the expectation is 18·2 : 18·2 : 4·6.
5. That all the F_2 glabrous plants will breed true to glabrousness. [All presumably contain H and K, and in respect of surface character are of one kind in composition as well as in appearance, and in character of offspring by self-fertilisation.]	Thirty-five glabrous F_2 plants were self-fertilised, and yielded *all* (750) *glabrous* offspring.
6. That the F_2 glabrous plants, which occur under two forms (whites and creams) will consist as regards the plastid character of the three Mendelian categories DD, DR (whites), and RR (creams).	Creams have already been shown to breed true. Of 33 F_2 glabrous whites, 24 when self-fertilised gave a mixture of white and cream, nine gave whites only.
7. That the group of non-sap-coloured plants (in this case identical with the glabrous group) will be composed in respect of the sap-colour character of five kinds of individuals: those containing C, of which some will be homozygous, some heterozygous: others containing R, similarly of two kinds homozygous and heterozygous: and, lastly, others containing neither C nor R. Further, that these five classes of individuals will occur among whites and creams alike.	Thirty-one F_2 whites were tested against seven F_2 creams in 35 different combinations. Two cases in which the number of offspring did not exceed three may be disregarded. Of the rest, one mating gave all sap-coloured hoary, 20 gave all non-sap-coloured glabrous, and 12 gave a mixture of the two (see Table IV).
If this be so, it follows that though *any* F_2 white or cream will breed true as regards the sap and surface characters when *self*-fertilised, some, when crossed together, will yield all hoary sap-coloured; others will yield all	

EXPECTATION (see Argument, p. 38, and fig. 3, p. 40)—*contd.*	RESULTS OBSERVED (see Detailed Analysis, Table III, p. 49, and Table IV, p. 52)—*contd.*
glabrous non-sap-coloured; others, again, will yield a mixture of the two. The relative frequency of the three kinds of matings will be 2, 31, and 16 respectively (see fig. 3, p. 40).	Observed frequency of matings 1, 20, and 12 respectively.
8. That in such matings *some* glabrous individuals (whether white or cream) will sometimes give one result, sometimes another, according to the constitution of the particular individual with which they are bred; whereas *others* will invariably give the same result (*cf.* type of sq. 16, fig. 3, p. 40).	Of the seven creams employed, one gave a total offspring of only eight, and may therefore be disregarded. Of the remaining six, four when bred with some whites gave *a mixture* of hoary and glabrous, but with others gave *all glabrous;* one sometimes gave *a mixture* and sometimes *all hoary;* one *always* gave glabrous only (10 matings) (see Table IV).
9. That when the F_2 glabrous plants are crossed with either of the original pure glabrous types the offspring will be *all hoary, all glabrous, or a mixture of the two,* according to the constitution of the particular F_2 individual.	Two matings with pure-bred whites gave *all hoary;* eight matings with pure-bred creams gave *all glabrous*, and one gave *a mixture.* It happened that one of the two bred with pure white was one of the eight bred with pure cream; it must therefore have been a homozygous type containing R but not C (*cf.* sq. 6, fig. 3, p. 40). (For details of experiment, see Table IV.)

The gametic composition of the glabrous strains, white, cream, red, being thus made clear, it remains to consider the hoary types, purple and white *incana* and white Bromptons. The mating purple *incana* and cream glabrous we may represent as CRBHK × cRbHK. Redistribution of these factors should give the following result: A mixed F_2 composed of hoary and glabrous, sap-coloured and non-sap-coloured, selfs and bicolours, purples and reds, whites and creams. In these all the hoary are sap-coloured and all the glabrous non-sap-coloured, and the ratio between the two contrary characters constituting a pair is in each case 3 : 1. The facts were as follows: From 4 fruits gathered from an F_1 cross-bred, 46 brown, 47 intermediate and 126 green seeds were obtained. Of the plants raised from green seeds 92 flowered and gave 79 purple selfs and 13 bicolours; 34 red selfs and 7 bicolours, 32 whites and 11 creams were obtained from the intermediate and the brown seeds respectively. We thus get the following results:—

173 hoary	46 glabrous	= 3 : 0·8
173 sap-coloured.........	46 non-sap-coloured ...	
126 purple	47 reds	= 3 : 1·1
113 self sap-colours ...	20 bicolours	= 3 : 0·5
32 white	11 creams	= 3 : 1·0

We again notice a distinct deficiency of cream forms (bicolours), otherwise the results accord with expectation. It may be that a further complication, apart from the late flowering habit of the cream forms, is here indicated, but owing to the fact that a certain proportion of the hoary plants failed to flower before the end of the season this point must, at present, remain undecided.

From "white" *incana* × cream glabrous we get the same series in F_2 as from purple *incana* × cream glabrous, with white and cream hoary in addition (see Rep. II, p. 18). But, as stated in the Introduction, "white" *incana* is undoubtedly a coloured form in reality, and the tinging which may be seen in fading flowers reappears in both hoary and glabrous F_2 whites from white *incana* × sap colours. On the other hand, in F_2 from white *incana* × cream (a genuine non-sap-coloured form) the hoary whites and creams tinge, but the glabrous plants give no sign of coloration on fading, and are evidently truly colourless in regard to sap. The case of white Bromptons, which give no visible indication of colour on fading, needs further investigation.

In the matings between hoary and glabrous forms, as with unions between two glabrous strains, the constitution of the F_2 plants is revealed by further breeding, and several types, otherwise indistinguishable, have been experimentally recognised in this way.

We can now comprehend more clearly the significance of the results in an earlier experiment (Rep. II, p. 9, Experiments 17A and 17B). Two F_2 glabrous whites from cream glabrous × white *incana* gave *all hoary* when crossed with pure-bred glabrous white. Of these two individuals one gave *all glabrous* when crossed with pure-bred glabrous cream. Both F_2 plants carried RHK (for both parent types contain these factors) but not C (otherwise they themselves would have given evidence of colour).

But pure-bred glabrous white carries CHK, hence when mated with *any* such glabrous F_2 white (or cream) or its descendants, the offspring will be *all hoary*. Conversely, any such F_2 glabrous plant or any of its descendants × a pure-bred cream similar to the parent cream will give *all glabrous*, for neither carry C. Further, *any* two such F_2 glabrous plants (whether white or cream) when mated together will give *all glabrous*. In fact, the results of Experiments 17A and 17B are to be regarded as holding not merely for particular individuals but for all the glabrous members of the F_2 family. Evidence fully bearing out this statement is furnished by the following experiments: 16 F_3 whites from 5 F_2 white parents of parentage similar to those employed in the above experiments, mated with a pure-bred cream gave 128 glabrous: 12 of these same F_3 whites descended from 4 of the 5 F_2 plants, crossed with an F_3 cream, gave 101 plants all glabrous.

Double Flowers.—The occurrence and distribution of double flowers has already been recorded in detail (Rep. II, p. 29). In the case of unions between glabrous strains the results were such as to suggest that no white, cream (excluding Princess May), or flesh-coloured plant used in these matings was throwing doubles, but that individuals belonging to other sap-coloured strains, notably the red, were undoubtedly giving off doubles. These strains have now been further tested, and the results are in accordance with the above supposition. No doubles were obtained from the white, cream or flesh-coloured strains in either of the two succeeding generations; on the other hand, the red race yielded doubles in abundance. From one red plant, 13 singles and 9 doubles were obtained in the first generation; 11 of these singles gave 134 singles and 200 doubles in the next generation; the doubles occurred in *every* family, and in most cases were in excess of the singles.

Taken all together the facts point to the following conclusions:—

(1) Doubles only occur in F_1 when both parents are throwing doubles, viz., are heterozygous. In F_2 they may not only occur when this is the case, but also when only one parent is heterozygous. When both parents are homozygous they are absent altogether. On this view the results of Experiments 15, 16, 19D, and 19E (Rep. II, pp. 8, 13, 35, 37) fall into line; red glabrous × dark purple glabrous gave doubles in F_1—both were, therefore, heterozygous. Since the same dark purple glabrous × light purple glabrous gave no doubles in F_1, the light purple was, therefore, presumably homozygous; doubles should, however, appear in F_2, and this was the case.

(2) Purple and white *incana* and all the white and cream glabrous plants hitherto used, Princess May excepted, have been homozygous.

(3) The sap-coloured glabrous strains employed probably comprised both homozygous and heterozygous individuals. The reds examined have so far proved to be all heterozygous, but in the case of the flesh-coloured race heterozygous individuals were evidently used in some unions with *incana* (Rep. II, Experiment 29, Table II, p. 33, also Experiment 31C),* homozygous plants in other matings with *incana* (*loc. cit.*, Experiment 1 (1)), and in all matings with glabrous races (Rep. II, pp. 37, 38).

As yet, however, we are without explanation of the remarkable fact that heterozygotes frequently yield a large excess of the latent form.

Experiments with M. sinuata.—From a mating between *sinuata* var. *glabra* and the type-form 12 hoary cross-breds were obtained in F_1 (see Rep. II, p. 39). Self-fertilisation of one of these cross-breds gave the expected mixture of hoary and glabrous plants in F_2, showing that in this species hoariness and glabrousness are related to one another precisely as in *incana*.

In another experiment a cross was made between the glabrous variety of *sinuata* and white *incana*; only 3 plants were obtained, and of these only 2 were raised to maturity. These plants (as stated in Rep. II, p. 40) were at first destitute of the stalked glands characteristic of *sinuata*, but examination of the plants in the second season showed a few scattered glands on the stem, pedicels, calyx, and ovary; on the leaves they were absent or very rare, whereas in pure *sinuata* they are abundant on all these parts. It, therefore, appears that gland formation in such cross-breds, though comparatively slight and of late occurrence, is not wholly absent as is the case with a strictly recessive character. The flowers and fruits were of the *sinuata* type, the corolla being small and with narrow petals, the pods slightly contracted between the seeds.

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* *Cf.* Corrigenda, Report III.

Another family of *sinuata-incana* cross-breds was obtained by mating extracted cream glabrous (an F_3 plant from cream glabrous × white *incana*) with a *sinuata* cross-bred (an F_1 plant from *sinuata* var. *glabra* × *sinuata* type). Five plants were obtained, of which 2 flowered. Glands were very numerous on the stem, pedicels, and calyx, less abundant on the ovary, and very scarce on the leaves. As in the cross-breds of the preceding experiment, the leaves were intermediate as regards outline and character of tomentum between the parent species, but in this case the corolla resembled *incana* both in size and shape of petals. Though the cross in the earlier experiment was between the pure-bred types, and in the present case between an extracted individual and a cross-bred, the one parent was in each case wholly of *sinuata*, the other of *incana* descent. The structural differences between the two F_1 families require further investigation.

Table I.—F_2 from Matings between Glabrous Strains.

Mating.	Numbers observed.		Expectation.		
	Hoary.	Glabrous.	Hoary.	Glabrous.	Ratio.
White × cream ……	128	95	126	98	9 : 7
White × sap-colours	169	103	153	119	9 : 7
Cream × sap-colours	284	188	265	206	9 : 7
	Sap-coloured glabrous.	Non-sap-coloured glabrous.	Sap-coloured glabrous.	Non-sap-coloured glabrous.	
White × cream ……	0	75	0	75	0 : all
White × sap-colours	37	41	33	44	3 : 4
Cream × sap-colours	82	95	76	101	3 : 4
	Non-cream.	Cream.	Non-cream.	Cream.	
White × cream ……	59	16	56	19	3 : 1
Cream × sap-colours	82	13	71	24	3 : 1

White Glabrous × Cream Glabrous, and Relative Number of each.

* An asterisk indicates that the form thus marked has been experimentally recognised.

Relative numbers of F_2 types.	Colours of F_2 types.	Colours yielded in F_3 by the several F_2 types.									
		Purple self.	Purple bicolour.	Plum self.	Plum bicolour.	Red self.	Red bicolour.	Copper self.	Copper bicolour.	White.	Cream.
*64	Purple self	+	+	+	+	+	+	+	+	+	+
*32	,,	+		+		+		+		+	
*32	,,	+	+	+	+					+	+
32	,,	+	+			+	+			+	+
*16	,,	+		+						+	
16	,,	+				+				+	
*16	,,	+	+							+	+
8	,,	+	+	+	+	+	+	+	+		
8	,,	+								+	
4	,,	+	+	+	+						
4	,,	+	+			+	+				
*4	,,	+		+		+		+			
2	,,	+		+							
2	,,	+				+					
2	,,	+	+								
1	,,	+									
*32	Purple bicolour		+		+		+		+		+
*16	,,		+		+						+
16	,,		+				+				+
8	,,		+								+
4	,,		+		+		+		+		
2	,,		+		+						
2	,,		+				+				
1	,,		+								
*32	Plum self			+	+			+	+	+	+
*16	,,			+	+					+	+
16	,,			+				+		+	
8	,,			+						+	

Table II—*continued*.

* An asterisk indicates that the form thus marked has been experimentally recognised.

Relative numbers of F_2 types.	Colours of F_2 types.	Colours yielded in F_3 by the several F_2 types.									
		Purplo self.	Purple bicolour.	Plum self.	Plum bicolour.	Red self.	Red bicolour.	Copper self.	Copper bicolour.	White.	Cream.
4	Plum self			+	+			+	+		
*2	,,			+				+			
2	,,			+	+						
1	,,			+							
*16	Plum bicolour				+				+		+
8	,,				+						+
2	,,				+				+		
1	,,				+						
*32	Red self					+	+	+	+	+	+
16	,,					+	+			+	+
*16	,,					+		+		+	
8	,,					+				+	
4	,,					+	+	+	+		
2	,,					+		+			
2	,,					+	+				
1	,,					+					
*16	Red bicolour						+		+		+
8	,,						+				+
2	,,						+		+		
1	,,						+				
*16	Copper self							+	+	+	+
8	,,							+		+	
*2	,,							+	+		
1	,,							+			
8	Copper bicolour								+		+
*1	,,								+		

Table III.—Analysis of F_3 Generation derived from Sap-coloured F_2 Plants in the Operation [(Cream Glabrous × White Glabrous) × Self] × Self.

Colour of F_2 plants.	Reference No. of F_2 plant.	Analysis of F_3 families.												
		Surface character.			Colour of hoary plants.								Colour of glabrous plants.	
		Hoary.	Glabrous.	Ratio of H : G.	Purple self.	Purple bicolour.	Plum self.	Plum bicolour.	Red self.	Red bicolour.	Copper self.	Copper bicolour.	White.	Cream.
Purple self …………	1	91	75	9 : 7·4	32	8	23	3	15	4	1	2	59	16
	2	138	120	9 : 7·8	44	14	26	10	24	3	13	2	87	31
	3	127	100	9 : 7·1	52	7	31	2	16	3	4	0†	90	8
	4	209	73	3 : 1·0	80	6	42	18	30	5	12	1	59	10
	5	74	53	9 : 6·4	25	9	14	1	14	3	6	0	40	12
	6	164*	108*	9 : 5·9	72	26	35	10	—	—	—	—	75	25
	7	173*	124*	9 : 6·4	64	19	31	3	—	—	—	—	86	24
	8	108*	32*	3 : 0·9	49	18	25	5	—	—	—	—	22	9
	9	81*	71*	9 : 7·9	24	5	6	0	—	—	—	—	21	5
	10	120*	95*	9 : 7·1	76	15	—	—	—	—	—	—	75	21
	11	152	107	9 : 6·3	79	—	32	—	26	—	10	—	106	—
	12	234	58	3 : 0·7	109	—	45	—	40	—	24	—	55	—
	13	164	—	all : 0	100	—	16	—	33	—	11	—	—	—
	14	178*	54*	3 : 0·9	97	—	53	—	—	—	—	—	46	—
Purple bicolour ……	15	76	40	?		29	—	11	—	7	—	5	—	—
	16	176*	54*	3 : 0·9		33	—	21	—	—	—	—	—	26
	17	208*	57*	3 : 0·8		41	—	16	—	—	—	—	—	12

* In the case of purples which do not yield the red classes, the proportion of hoary and glabrous can be calculated from the seed colour; all numbers thus obtained are marked with an asterisk.

† Absence of a form, due presumably to the small total, is indicated by 0, in other cases by a —.

Table III—*continued.*

Colour of F_2 plants.	Reference No. of F_2 plant.	Analysis of F_3 families. Surface character.			Colour of hoary plants.								Colour of glabrous plants.	
		Hoary.	Glabrous.	Ratio of H : G.	Purple self.	Purple bicolour.	Plum self.	Plum bicolour.	Red self.	Red bicolour.	Copper self.	Copper bicolour.	White.	Cream.
Plum self	18	170	61	3 : 1·1			108	19	—	—	35	0	49	8
	19	172	47	3 : 1·0			98	26	—	—	25	10	37	8
	20	176	70	3 : 1·2			79	22	—	—	47	6	49	7
	21	119	42	3 : 1·0			55	17	—	—	18	3	28	9
	22	45	12	3 : 0·8			35	10	—	—	—	—	10	2
	23	138	46	3 : 0·9			106	24	—	—	—	—	28	6
	24	112	37	3 : 1·0			86	24	—	—	—	—	33	2
	25	219	—	all : 0			140	—	—	—	47	—	—	—
	26	144	—	all : 0			100	—	—	—	35	—	—	—
Plum bicolour	27	134	53	3 : 1·2				94	—	—	—	—	—	24
Red self	28	101	36	3 : 1·1					58	12	23	4	26	8
	29	152	116	9 : 6·9					77	17	35	14	96	12
	30	66	50	9 : 6·8					42	4	13	8	42	8
	31	53	20	3 : 1·1					21	11	12	3	14	5
	32	80	36	3 : 1·3					54	—	24	—	36	—
	33	33	10	3 : 0·9					20	—	10	—	9	—
Red bicolour	34	48	41	9 : 7·7						28	—	15	—	41
	35	50	40	9 : 7·2						31	—	17	—	39
	36	13	4	3 : 0·9						7	—	3	—	4
	37	66	57	9 : 7·8						31	—	21	—	47

Copper self…………	38	60	16	3 : 0·8							44	8	11	1
	39	54	23	3 : 1·3							42	8	18	2
	40	22	6	3 : 0·8							14	4	4	0
	41	62	—	all : 0							51	4	—	—
Copper bicolour……	42	115	—	all : 0								100	—	—

Conclusions in regard to F_2 Plants analysed in Table III.

Reference No. of plant.	Factors and characters as to which the plant is heterozygous.	Factors and characters as to which the plant is homozygous.
1, 2, 3, 5	C, R, B, plastid colour, quality of sap-colour	H, K
4	C (or R), B ,, ,, ,, ,,	R (or C) H, K
6, 7, 9	C, R ,, ,, ,, ,,	B, H, K
8	C (or R) ,, ,, ,, ,,	R (or C), B, H, K
10	C, R, plastid colour	B, H, K, quality of sap-colour (full)
11	C, R, B, quality of sap-colour	H, K, plastid colour (white)
12	C (or R), B, quality of sap-colour	R (or C), H, K, plastid colour (white)
13	B, quality of sap-colour	C, R, H, K, plastid colour (white)
14	C (or R), quality of sap-colour	R (or C), B, H, K, plastid colour (white)
15	B, quality of sap-colour. ? C, R	H, K, plastid colour (cream)
16, 17	C (or R), quality of sap-colour	R (or C), B, H, K, plastid colour (cream)
18—21	C (or R), B, plastid colour	R (or C), H, K, quality of sap-colour (modified)
22—24	C (or R), plastid colour	R (or C), B, H, K, quality of sap-colour (modified)
25, 26	B	C, R, H, K, plastid colour (white), quality of sap-colour (modified)
27	C (or R)	R (or C), B, H, K, plastid colour (cream), quality of sap-colour (modified)
28, 31	C (or R), plastid colour, quality of sap-colour	R (or C), b, H, K
29, 30	C, R, plastid colour, quality of sap-colour	b, H, K.
32, 33	C (or R), quality of sap-colour	R (or C), b, H, K, plastid colour (white)
34, 35, 37	C, R, quality of sap-colour	b, H, K, plastid colour (cream)
36	C (or R), quality of sap-colour	R (or C), b, H, K, plastid colour (cream)
38—40	C (or R), plastid colour	R (or C), b, H, K, quality of sap-colour (modified)
41	Plastid colour	C, R, b, H, K, quality of sap-colour (modified)
42		C, R, b, H, K, plastid colour (cream), quality of sap-colour (modified)

Table IV.—Showing Different Results obtained from the *same* Glabrous F_2 Individual in Different Matings with other Glabrous Plants, both Extracted and Pure-bred.

	Analysis of F_3 families.	
	Surface character.	Plastid colour.
Matings between F_2 whites and F_2 creams.		
$W_1 \times C_1$	19 hoary	
$W_{10} \times C_2$	2 glabrous	Wh.
$W_{11} \times C_2$	6 ,,	Wh. and cr.
$W_{13} \times C_3$	38 ,,	Wh. and cr.
$W_{14} \times C_4$	46 ,,	Wh. and cr.
$W_6 \times C_5$	26 ,,	Wh.
$W_7 \times C_5$	6 ,,	Wh. and cr.
$W_8 \times C_5$	26 ,,	Wh. and cr.
$W_9 \times C_5$	16 ,,	Wh.
$W_{19} \times C_5$	13 ,,	Wh. and cr.
$W_{20} \times C_6$	21 ,,	Wh. and cr.
$W_{21} \times C_6$	28 ,,	Wh. and cr.
$W_2 \times C_7$	34 ,,	Wh. and cr.
$W_3 \times C_7$	3 ,,	Wh. and cr.
$W_4 \times C_7$	35 ,,	Wh.
$W_5 \times C_7$	18 ,,	Wh. and cr.
$W_{12} \times C_7$	33 ,,	Wh. and cr.
$W_{15} \times C_7$	9 ,,	Wh.
$W_{16} \times C_7$	21 ,,	Wh.
$W_{17} \times C_7$	34 ,,	Wh.
$W_{18} \times C_7$	26 ,,	Wh.
$W_{22} \times C_7$	41 ,,	Wh. and cr.
$W_{23} \times C_7$	33 ,,	
$W_4 \times C_1$	Hoary and glabrous	Wh.
$W_{22} \times C_1$	,, ,,	Wh. and cr.
$W_{24} \times C_1$	,, ,,	Wh.
$W_{14} \times C_3$	,, ,,	Wh. and cr.
$W_{19} \times C_4$	,, ,,	Wh. and cr.
$W_{25} \times C_5$	,, ,,	Wh. and cr.
$W_{26} \times C_5$	,, ,,	Wh. and cr.
$W_{27} \times C_5$	,, ,,	Wh. and cr.
$W_{28} \times C_5$	,, ,,	Wh.
$W_{29} \times C_6$	,, ,,	Wh. and cr.
$W_{30} \times C_6$	,, ,,	Wh. and cr.
$W_{31} \times C_6$	,, ,,	Wh. and cr.
Matings between F_2 whites and pure-bred creams.		
W_{12} × pure-bred cream	29 glabrous	Wh. and cr.
W_{13} × ,, ,,	9 ,,	Wh. and cr.

Table IV—*continued.*

	Analysis of F_3 families.	
	Surface character.	Plastid colour.
Matings between F_2 whites and pure-bred creams—*continued.*		
W_{17} × pure-bred cream ...	35 glabrous	Wh.
W_{21} × ,, ,, ...	28 ,, ...	Wh. and cr.
W_{29} × ,, ,, ...	17 ,, ...	Wh. and cr.
W_{30} × ,, ,, ...	34 ,, ...	Wh. and cr.
W_{31} × ,, ,, ...	48 ,, ...	Wh. and cr.
W_{32} × ,, ,, ...	6 ,, ...	Wh. and cr.
W_{18} × ,, ,, ...	Hoary and glabrous	
Matings between F_2 whites and pure-bred whites.		
W_{31} × pure-bred white ...	16 hoary	
W_{33} × ,, ,, ...	16 ,,	

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REPORTS TO THE EVOLUTION COMMITTEE OF THE ROYAL SOCIETY.

REPORT IV.

EXPERIMENTAL STUDIES IN THE PHYSIOLOGY OF HEREDITY.

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The present Report deals with the continuation of the experiments with Poultry, Sweet Peas, and Stocks.

Some account is given of our analysis of the various kinds of white plumage in fowls. We have been able to show that, in addition to the white which is dominant to colour, there are two entirely distinct whites which severally behave as recessive to colour, but on crossing give only coloured birds.

In our last Report we gave reasons for regarding the rose-comb as a comb on which an additional element, "roseness," had been superposed, and we suggested that the allelomorphic pair consists in the two states: presence of the factor for rose (R) and absence of that factor (r). The rose-comb is in reality a single comb modified by the presence of a "rose" factor. The omission of this factor enables the single comb to appear. The same considerations apply to the pea-comb, which is single + a pea factor. The true allelomorphic pair in each case is the *presence* of a given factor which is dominant to the *absence* of that factor. This view we have since been able to illustrate by another experiment (p. 18), and recent experience inclines us to regard it as applicable to all Mendelian cases as yet investigated. As the acceptance of the "Presence and Absence" hypothesis seems to demand some general expression for such inter-relation between factors belonging to distinct allelomorphic pairs, we propose the terms *epistatic* and *hypostatic.** For example, the combless, the single-combed, and the rose-combed conditions may, in the light of our present knowledge, be regarded as forming a cumulative series, and we should speak of the factor for single as being dominant to the combless condition but hypostatic to the rose factor; and similarly the rose factor may be referred to as epistatic to the single.

Some experiments with Sweet Peas have led to an extension of our knowledge of the inheritance of stature in this species. A cross was made between the dwarf procumbent "Cupid" and a half-dwarf form known as the "Bush" Sweet Pea. The F_1 plants all "reverted" to the normal tall habit, and subsequent breeding from these demonstrated clearly that the case can be expressed as one of simple dihybridism (see p. 6).

The majority of our Sweet Pea work of the past two seasons was undertaken with a view to further elucidating the phenomenon we have

* Already suggested by one of us in 'Science,' November 15, 1907.

termed gametic coupling. Experiments described in our last Report showed that the offspring of plants heterozygous for the blue factor and for long pollen can be classified (omitting the whites) as purples and reds in the ratio 3 : 1, and as plants with long and round pollen in the same ratio. But the distribution of the pollen among the coloured forms was complex. Instead of there being three long purples to each round one there were actually about twelve; and the deficiency of rounds among the purples was compensated for among the reds, where they were three to four times as numerous as the longs. We pointed out that this peculiar distribution would be brought about if we supposed that the majority of purple-bearing gametes bore also the factor for long pollen, and that the corresponding majority of non-blue gametes were associated with roundness. We suggested that in the present case the choice lay between the following two gametic series from the F_1 plant:—

(*a*) 8 purple long, 1 purple-red, 1 red long, 8 red round.
(*b*) 7 ,, 1 ,, 1 ,, 7 ,,

The comparative merits of these two systems were discussed in Report III, and we are still unable to decide finally between them. The numbers, hewever, are somewhat more consistent with the scheme based on the 7 : 1 : 1 : 7 ratio.

During the past two years we have come across two cases among Sweet Peas in which the coupling is closer. One of these also relates to the factors for purple and pollen shape (p. 11), but the other has to do with two entirely different pairs of factors, viz., dark and light axil, and fertile as opposed to sterile anthers (p. 16). In both of these instances the distribution of characters in F_2 is in accordance with the view that the gametic series is on a 15 : 1 : 1 : 15 basis.

The undoubted existence of these two grades of gametic coupling in the Sweet Pea suggests that each may find its place in a scheme of increasing intensity of gametic coupling, such as is shown in the accompanying table, where the two allelomorphic pairs are represented by Aa and Bb:—

Gametic series.					Zygotes containing—				
AB.	Ab.	aB.	ab.		A and B.	A only.	B only.	Neither A nor B.	
1	: 1	: 1	: 1	= 4	9	: 3	: 3	: 1	= 16
3	: 1	: 1	: 3	= 8	41	: 7	: 7	: 9	= 64
7	: 1	: 1	: 7	= 16	177	: 15	: 15	: 49	= 256
15	: 1	: 1	: 15	= 32	737	: 31	: 31	: 225	= 1024
$n-1$	: 1	: 1	: $n-1$	$= 2n$	$3n^2-(2n-1)$	: $2n-1$	: $2n-1$	: $n^2-(2n-1)$	$= 4n^2$

The first term in the series is a simple case of dihybridism in which no coupling exists. The second term we have not yet encountered. But we have an ample series of experimental data which satisfy the third term; and the experimental evidence for the existence of the fourth term rests upon two independent cases.

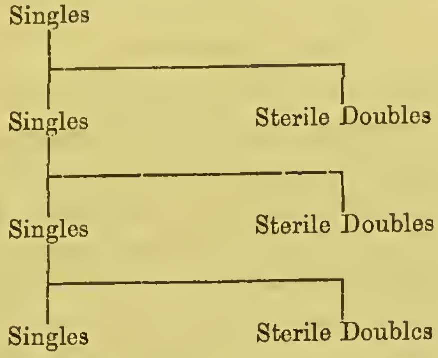
As we have indicated in the table above, there is a general expression for this series of terms. If the number of the gametic series be represented by $2n$, then the number of zygotes formed by such a series is $4n^2$; and this number will be distributed in such a way that there will be $3n^2-(2n-1)$ zygotes with both dominants, two groups of $2n-1$ with one dominant each, and $n^2-(2n-1)$ with neither dominant. It is obvious that, as the value of n increases, the terms containing n become relatively smaller in comparison with those containing n^2. The closer the gametic coupling the rarer become the two middle terms of the series which contain but one dominant apiece. And if n become very large, it is clear that the series

$$3n^2-(2n-1) : 2n-1 : 2n-1 : n^2-(2n-1)$$

will approximate to the series $3n^2 : 0 : 0 : n^2$. In other words, the greater the value of n, the closer we approach to a simple 3 : 1 ratio. When aberrant forms occur in a series which is apparently of the usual 3 : 1 type, it may be worth while examining them with a view to the possibility that they may represent the scarcer terms in a series resulting from close coupling.

During the past two seasons much of our time has been devoted to the inheritance of the hooded character in the Sweet Pea. The hooded standard behaves as a recessive to the erect standard, but in certain strains containing both red and purple flowers the hood is always associated with the latter colour (p. 9). In such cases we must suppose that all the "red" gametes bear the factor for the erect standard, and that this factor is absent from all the gametes which carry purple. We have, in Report III, referred to this phenomenon as one of gametic coupling, but strictly this expression is inapplicable. In the cases of actual gametic coupling discussed in the last paragraph the association is always between the dominant or *present* factors of the different pairs; long pollen is coupled with purpleness, and the dark axil with the fertile anther. The "present" factors would seem to behave in gametogenesis as though they were attracted by one another. But here the phenomenon is of a different order. The two dominant factors, blueness and erect standard, seem to repel one another so that they are not both found in the same gamete; consequently only two kinds of gamete are produced instead of the four characteristic of a normal case of dihybridism, and the result is a simple 1 : 2 : 1 ratio such as we should obtain when dealing with a simple Mendelian pair. For this phenomenon we suggest the term *spurious allelomorphism.*

In Stocks, the work has been chiefly concerned with the inheritance of double flowers. The experiments have brought to light a phenomenon of a new order. Double Stocks being always totally sterile, both as regards male and female organs, are invariably the offspring of single-flowered plants. The succession in these double-throwing strains of singles is thus to be represented as follows:—



Though always the offspring of singles, the doubles are nevertheless the majority, and the genetic mechanism by which this remarkable succession is accomplished remains problematical. The experiments have, however, contributed a first step towards the solution. *Singleness* is an ordinary Mendelian dominant to *doubleness* (Reps. III, p. 44, and II, p. 29), but the singles in the double-throwing strains are of a curious composite nature. The double-throwing singles were crossed reciprocally with a strain of pure singles. The F_1 plants are all alike single; but an examination of F_2 from these plants revealed a remarkable difference between the results of the reciprocals.

For where the pure single was used as mother, F_2 from each F_1 contained doubles, whereas when pure single was the father, some of the F_2 families contained doubles and some were all singles. It follows therefore that the pollen-grains of the double-throwing strains must be all or nearly all* bearers of doubleness; but that the egg-cells are of two kinds, those that bear singleness and those that bear doubleness.

The transmission of the cream-colour in the case of those single whites (known as "sulphur-whites") which throw double creams follows a similar system. The pollen-grains of such plants are all or nearly all* bearers of cream-colour, but the egg-cells are of two kinds, those which bear cream-colour and those which bear whiteness.

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* Pending further inquiry, these statements must not be made in a universal form. Though hitherto no exception has been found in either case, it is still quite possible that a small proportion of the pollen-cells in each case bear the dominant character.

SWEET PEAS.

(Experiments by W. Bateson and R. C. Punnett.)

Bush × Cupid Cross.

The Bush Sweet Pea, a form not previously used in these experiments, has a peculiar conformation. After reaching a height of about 8 inches it branches profusely from its lower nodes. Of the stems thus formed about 10—15 grow on, eventually reaching a height of some 3½ feet. The production of branches continues, but those formed later remain short and slender. In an ordinary tall Sweet Pea only about four or five stems attain any considerable extension (without special treatment). The stems of the Bush are thin and rather wiry, especially at the base, and the plants, till they reach a height of about 18 inches, can almost maintain themselves erect without sticks. By that time the stems are mutually entangled by their tendrils, and the compact bush-like form is very pronounced, entirely distinguishing them from any other sort of Sweet Pea.

In both the ordinary tall plants and the ordinary Cupids there appears to be some factor which restrains the production of branches, and thus enables the plant to attain a greater length. The non-branching tall plant attains a height 2 or 3 feet greater than that of the Bush, which must be regarded as a branching "tall." Similarly, the erect or branching Cupid is more stunted in its length than the ordinary or non-branching Cupids. The allelomorphs concerned are evidently:—

Dominant.	Recessive.
1. Tallness (T).	Dwarfness (t).
2. Prostrate: non-branching (P).	Erect: branching (p).

The ordinary tall is TTPP, the prostrate Cupid is ttPP, and the Bush is TTpp. When Bush is crossed with Cupid the two complementary factors, T and P, necessary to the production of the full height, meet each other and the "reversion on crossing" occurs.

In F_2, besides the three forms already mentioned with which we were familiar, there appears also, in consequence of the recombination of the factors, a new type—the erect dwarf (ttpp). These little plants have a very singular appearance, being extremely short and erect, somewhat resembling box-edging.

The numbers in the F_2 generation from six F_1 plants were:—

	Observed.	Calculated.
Tall (= prostrate talls)	219	*217·8*
Bush (= erect talls)	70	*72·5*
Prostrate Cupids	69	*72·5*
Erect Cupids	29	*24·2*
	387	*387*

The observed numbers approach closely to those calculated on the 9 : 3 : 3 : 1 ratio, and the case is evidently one of dihybridism in which the two pairs of factors concerned are those we have suggested above.

The families resulting from this cross are considered elsewhere (p. 12) in connection with gametic coupling.

Table I.

	Tall.	Bush.	Cupid prostrate.	Cupid erect.		
Purple erect long	54	18	10	1	83	184 [167]
Purple erect round	4	—	1	1	6	
Purple hood long	24	11	5	8	48	
Purple hood round	—	—	—	—	—	
Red ... long	3	2	—	—	5	
Red ... round	23	11	6	2	42	
White erect long	43	10	10	3	66	113 [130]
White erect round	11	2	1	3	17	
White hooded long	20	5	4	1	30	
White hooded round	—	—	—	—		
Colour and pollen unknown*	37	11	32	10		
Total	219	70	69	29		
Expectation	217·8	72·6	72·6	24·2		

* Owing to late germination and consequent failure to flower.

The Inheritance of the Hooded Character.

The work of the past two seasons has consisted largely in the investigation of the peculiar transmission of the hooded standard. The hood is constituted by a more or less pronounced folding downwards of the top and sides of the standard or vexillum† (*cf.* fig,. p. 8). The hooded varieties may be of almost all the colours known in Sweet

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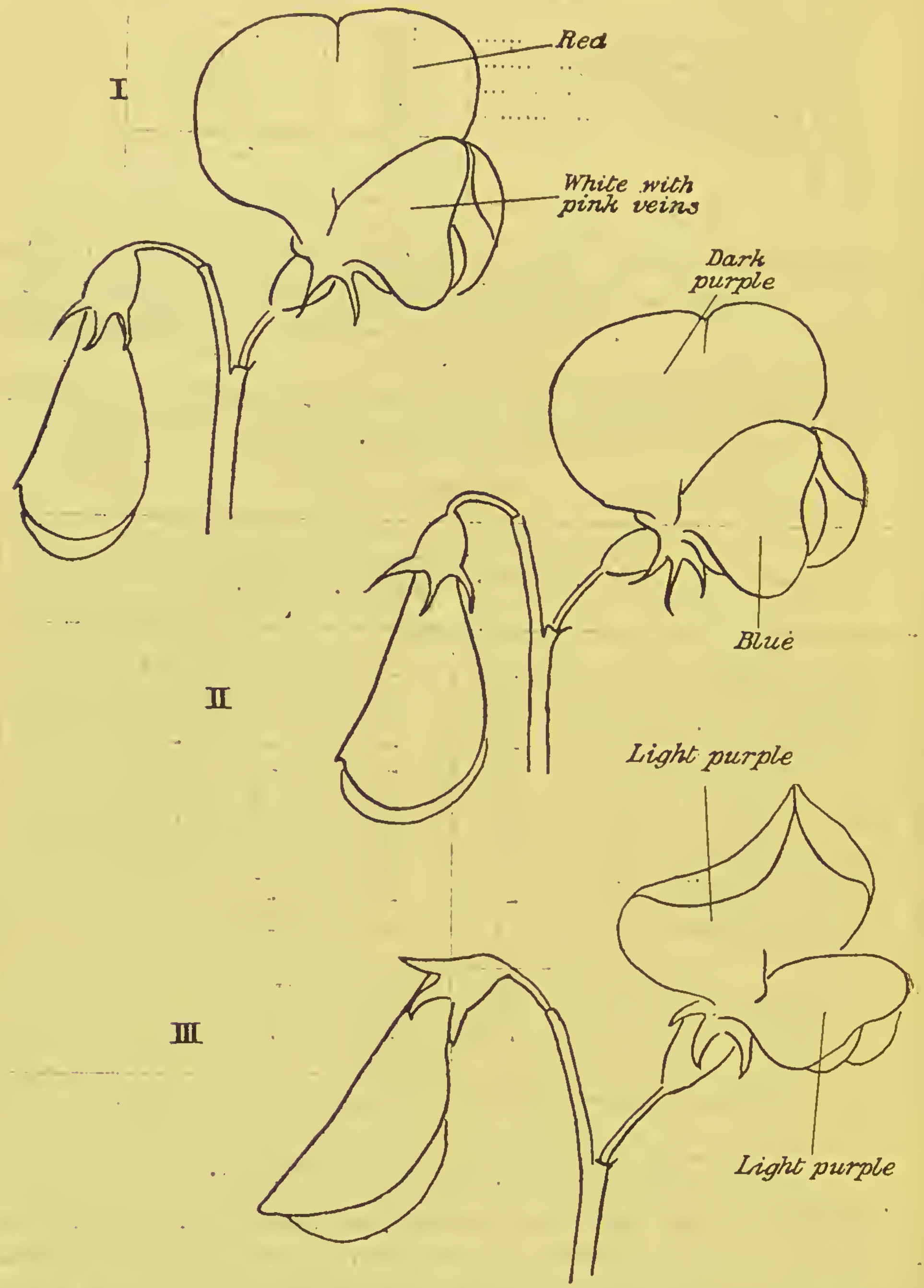
† This shape is associated with, and perhaps caused by, absence of the central notch which is conspicuous in the middle of the erect standard of old-fashioned flowers. The shape of the buds in the two types is consequently very distinct (see figures).

Peas—white, cream, red, pink, mauve, purple—but, so far as we have observed, the hood never occurs in the purple bicolor or Purple Invincible (P. I.), or in the corresponding red bicolor or Painted Lady (P. L.). In all the hooded types standard and wings are more alike in tint; and there is therefore some interdependence between



Diagrammatic representation of the three coloured types which occur in F_2 from Blanche Burpee (hood white) × E. Henderson (erect white), giving F_1 purple erect. I. Painted Lady; II. Purple Invincible; III. Duke of Westminster.

colour and form such that either the bicolor character prevents the development of the hood, or the development of the hood modifies the colour.* The erect type of standard is dominant to the hooded type.

The original cross with which we started was made in 1904 between the two whites, Blanche Burpee (long pollen, hooded) and Emily Henderson (round pollen, erect standard). The majority of the F_1 plants were P. I. (some being whites, others P. L., according to the factorial composition of the parents), and it is from such plants and their offspring that the data put together in Table II were obtained. From the four F_1 plants 773 plants were raised in F_2, with the following results :—

Erect purples.	Hooded purples.	Erect reds.	Whites (erect and hooded).
232	83	112	346
315 [326]		[109]	[338]
427 [435]			

As was to be expected, the purples are three times as numerous as the reds, and the coloured are to the whites as 9 : 7. From the F_2 generation families were raised in F_3 and F_4, as is recorded in Table II. The striking feature about this series of experiments is that among the *coloured* flowers hoods are only found on the purples. Among some thousands of plants, not a single hooded red has appeared. Nevertheless, the existence of hooded red types is well known in Sweet Peas. We are therefore led to suppose that we are dealing with a strain in which the factor for erect standard is alternative in the gametes to the factor for blue : and, conversely, that every gamete which carries the factor for the erect standard is devoid of the blue factor. Consequently, for these two pairs of factors, only two of the four conceivable classes of gamete exist, viz., blue hooded gametes, and non-blue erect gametes. The spurious allelomorphism (see p. 4), which we must assume to exist between blue and hood on the one hand, and between non-blue and erectness on the other, does not allow of the formation of purple erect, or of red hooded gametes. If this assumption is correct, there should follow certain consequences which may be tested by the data given in Table II.

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* The purple hooded types produced in these experiments are those known as Duke of Westminster and Duke of Sutherland respectively. The former corresponds with P. I., and the latter is represented among the erect types by the purple with purple wings referred to in these Reports as P.p.w.

The colour difference between hooded and flat types is not easy to express, but may readily be perceived when a collection of Sweet Peas is examined. In the erect purple and red bicolors the colour of the standard contains a red quality distinguishing it from that of the wings, which are more blue in the case of purples and more pink in the case of reds. While in a purple bicolor the standard is a chocolate red and the wings are blue or purple, the corresponding hooded type has both parts purple. Similarly in a red bicolor the colour of the standard is a scarlet and that of wings pink or pinkish-white, while in the corresponding hooded type the pigment of both parts is pink. When, as sometimes happens, the standard and wings of a hooded type differ in colour, the difference is rather in the amount of pigment than in its quality, the standard being fuller and the wings lighter, but the pigments of both parts show little difference in tint.

1. Every hooded purple must be homozygous for the blue factor.	In Experiments 48—53, six hooded purples, although from families in which reds occur, bred true to purple (except in so far as whites might appear).
2. Every red must be homozygous for the erect standard.	In Experiments 54—59, six reds were bred from, and proved to be all homozygous for the erect standard.
3. Every erect purple must be heterozygous for both the erect standard and for blueness, and must therefore give hooded purples, erect purples, and reds, in the ratio 1 : 2 : 1.	The erect purples, whose offspring are recorded in Experiments 1—47, all gave hooded purples and erect reds. Of their 3707 coloured offspring, 902 were hooded purples, 939 were erect reds, and 1920 were erect purples.
4. Every hooded white must be homozygous for the blue factor.	In the only two cases in which the cross between a hooded white and a red has succeeded, the coloured offspring have been purple. We hope to obtain further results in the present year.
5. Since every hooded plant is homozygous for purple, and since long pollen is partially coupled with the blue factor, it follows that round pollen should be much rarer among the hooded than among the erect purples.	So far only two round hooded purples and one round hooded white have been met with in families heterozygous for hood and purple (Experiments 1—47). With this point we shall deal later, in connection with partial coupling (see p. 13).

The phenomenon of association of hood with purple was also witnessed in the F_2 families resulting from the Bush × Cupid cross, with which we have already dealt in another connection (p. 2). Here, again, the hood occurred in F_2, and only on the purples. The numbers—48 hooded purples, 89 erect purples, and 47 erect reds—are very close to the expected ratio, 1 : 2 : 1.

As stated above, in other strains red hooded forms exist. Experiments with these types are in progress, but have not yet been carried far enough to give positive results.

Partial Gametic Coupling.

A. *Between Pollen and Colour.*—In our last Report (p. 9), we showed that the distribution of pollen characters, long grains and round grains, was affected by that of the colour characters, according to a definite system, and we pointed out that the experimental results were explicable on the assumption that in plants, heterozygous for colour and pollen, the gametes were produced in a series of 16, viz., 7 purple long, 1 purple round, 1 red long, and 7 red round. Purple is associated with long pollen and red with round, but in neither case is the coupling complete.

In the four F_1 families from the cross Blanche Burpee × Emily Henderson (Table II, Exps. 1—4), the distribution of the pollen fits in with this scheme, as the following numbers show :—

	Observed.	Expectation on the 7 : 1 : 1 : 7 basis.
Purple long	296	*295*
Purple round	19	*25*
Red long	27	*25*
Red round	85	*82*
	427	*427*

From one of these F_2 families (No. 2), ten erect purples were chosen and grown on in the following year (Nos. 5—14). They produced :—

	Purple long.	Purple round.	Red long.	Red round.
F_3 generation from No. 2...............	493	25	25	138
Expectation on 7 : 1 : 1 : 7 basis...	*471*	*40*	*40*	*130*
Expectation on 15 : 1 : 1 : 15 basis...	*490*	*20*	*20*	*151*

The number of round purples and of long reds is in each case decidedly lower than would be looked for on the assumption that the coupling was on a 7 : 1 : 1 : 7 basis, and is much nearer to what would be expected if the coupling were on a 15 : 1 : 1 : 15 basis. In some families, the dearth of these two classes is particularly well marked, and two of them (Nos. 5 and 6) were bred from. From No. 5, five families (Nos. 15—19) were obtained, and these, with the present plant, gave the following result :—

	Purple long.	Purple round.	Red long.	Red round.
No. 5 and its offspring, Nos. 15—19	545	25	40	159
Expectation on 7 : 1 : 1 : 7 basis...	*532*	*45*	*45*	*147*
Expectation on 15 : 1 : 1 : 15 basis...	*554*	*23*	*23*	*169*

The results are irregular. The proportion of red longs to red rounds fits fairly well with the supposition that the coupling is on a 7 : 1 : 1 : 7 basis; but the purple rounds are only half as many as would be expected. The coupling between long and purple seems to be closer, and is in accordance with the supposition that the gametic series is 15 : 1 : 1 : 15. Both in the F_3 generation and in these F_4 plants there is evidently some disturbing process which we cannot at present express, though it is possible that we are dealing with a mixture of families exhibiting the two forms of coupling.

From the other of the two F_3 plants chosen for further experiment (No. 6), we obtained a much more definite result. From it eight families, heterozygous in colour and pollen, were raised (Table II, Nos. 20—27). On adding together the results of these nine families, we obtain the following numbers :—

	Purple long.	Purple round.	Red long.	Red round.
No. 6 and its offspring, Nos. 20—27	583	26	24	170
Expectation on 15 : 1 : 1 : 15 basis...	*578*	*24*	*24*	*177*

It is obvious that the numbers in this group of families accord very closely with the figures expected on a 15 : 1 : 1 : 15 basis; and the view that this is the system actually followed receives confirmation from the distribution of the pollen and colour characters in the F_2 families from the Bush* × Cupid crosses (Table I, p. 7), where the following figures were obtained :—

	Purple long.	Purple round.	Red long.	Red round.
F_2 families ex Bush × Cupid	131	6	5	42
Expectation on 15 : 1 : 1 : 15 basis...	*132·4*	*5·6*	*5·6*	*40·4*

From the closeness with which the recorded results agree with expectation, it is evident that here again we are concerned with a 15 : 1 : 1 : 15 series. And when we come to deal with the inheritance of sterility in the Sweet Pea (p. 16), we shall meet with another case, in which we are undoubtedly concerned with a similar gametic series. We may take it, therefore, that there is good evidence for the existence of gametic coupling in the 15 : 1 : 1 : 15 series, as well as for the derivation of the families exhibiting the higher form from families in which the lower occurs. We have, then, to recognise that in some families the coupling follows one system and in others another. Each process is, nevertheless, definite. As yet, however, we have not perceived any circumstance to which the distinction can be attributed.

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* The flower of the Bush plants used was a hooded white, exactly like that of Blanche Burpee.

In an earlier paragraph (p. 10), we mentioned that, owing to the partial coupling of long pollen with purple, we should expect hooded purples and hooded whites to be found very rarely with round pollen. When the gametes are produced in series of 16, *i.e.*, 7 purple long, 1 purple round, 1 red long, and 7 red round, it is clear that the chances of two purple round gametes meeting are only 1 in 16^2, *i.e.*, in 256 in families where reds occur. Of these 256 plants, 64 are homozygous for purple. Consequently, the chances of a homozygous purple having round pollen are 1 in 64. In families where hoods occur all the homozygous purples are hooded, and we should, therefore, look for one round hooded purple in 64. In the four F_1 families (Nos. 1—4), 1 round hooded purple occurred among 83 plants. Again, since the hooded whites are homozygous for purple, on our view we should look for one with round pollen out of 64. Actually, one white hooded plant with round pollen occurred among the 18 F_2 families, where the hood was recorded (Nos. 1 and 4). Where expectation demands 1 in 64, experiment gave 2 hooded rounds in 101.

If, however, the coupling is on the 15 : 1 : 1 : 15 basis, the proportion of rounds among the hooded purples and whites should be only 1 in $32^2 \div 4$, *i.e.*, 1 in 256. In No. 6 and its descendants, Nos. 20—27, only one of the 209 hooded purples had round pollen.

These complicated facts may be summarised thus:—From an examination of the families where the hooded standard occurs, it is quite clear that in some of them the coupling of blue factor with long pollen is definitely distributed according to the system 15 : 1, and that in others it follows the system 7 : 1. There are also families which cannot confidently be referred to either class. Since the F_2 derived from Bl. Burpee by E.H. round followed the 7 : 1 system, the heterozygosis between erectness and hood cannot be regarded as the direct cause of the 15 : 1 distribution. The families showing that distribution came in F_3 and later generations from this cross, and the 15 : 1 system seems, therefore, to have been brought into operation by the omission of something which may be supposed to be carried on in those collateral families which follow the 7 : 1 system. Scrutiny of the various groups has, however, failed to discover any consistent difference between those of the 7 : 1 type and those of the 15 : 1 type. In the case of the Bush × Cupid cross the 15 : 1 system appeared at once in F_2.

Table II.

	Exp. number.	Reference number.	Purples, erect.		Purples, hooded.		Reds.		Whites, erect.		Whites, hooded.		Reference number of parent.
			long.	rd.	long.	rd.	long.	rd.	long.	rd.	long.	rd.	
Families from purple parent heterozygous in blue, hood, and pollen.	1	'05, 253	25	2	11	—	3	10	31	15	11	1	
	2	309	50	6	20	—	12	23	(65 long + 15 rd.)				
	3	310	118	8	36	1	8	41	(116 long + 36 rd.)				
	4	312	21	2	15	—	4	11	37	13	6	—	
	5	'06, 302	39	3	26	—	1	20	17	1	1	—	'05, 309
	6	305	55	4	33	—	1	33	—	—	—	—	"
	7	307	25	1	11	—	2	7	11	3	7	—	"
	8	363	9	2	7	—	3	7	4	2	1	—	"
	9	368	5	—	3	—	—	4	5	4	5	—	"
	10	370	4	1	6	—	2	5	2	1	—	—	"
	11	372	76	4	43	—	6	23	20	12	12	—	"
	12	374	69	5	34	—	5	27	25	13	15	—	"
	13	376	11	2	6	—	2	5	13	4	6	—	"
	14	377	23	3	8	—	3	7	8	3	2	—	"
	15	'07, 131	33	1	10	—	5	10	12	3	6	—	'06, 302
	16	132	78	6	44	—	12	30	27	13	13	—	"
	17	133	98	6	57	—	9	51	39	15	21	—	"
	18	134	33	4	15	—	3	13	—	—	—	—	"
	19	136	93	5	45	—	10	35	28	13	22	—	"
	20	137	31	6	23	—	2	23	—	—	—	—	'06, 305
	21	138	65	6	37	1	3	32	—	—	—	—	"
	22	139	24	1	10	—	3	13	—	—	—	—	"
	23	140	43	1	22	—	4	22	—	—	—	—	"
	24	141	73	1	31	—	5	21	—	—	—	—	"
	25	143	18	1	14	—	2	8	—	—	—	—	"
	26	144	37	4	22	—	3	7	—	—	—	—	"
	27	145	29	1	16	—	1	11	—	—	—	—	"

Families from purple parent heterozygous in blue and hood.	28	'06, 303	—	13	—	9	—	13	—	11	—	9	'05, 309
	29	304	65	—	32	—	31	—	45	—	8	—	,,
	30	310	—	22	—	8	—	15	—	9	—	3	,,
	31	365	29	—	2	—	11	—	20	—	4	—	,,
	32	371	35	—	13	—	14	—	—	—	—	—	,,
	33	'07, 135	—	17	—	9	—	10	—	6	—	2	'06, 302
	34	142	33	—	17	—	18	—	—	—	—	—	305
	35	146	28	—	12	—	12	—	—	—	—	—	304
	36	147	20	—	8	—	10	—	5	—	3	—	,,
	37	148	35	—	12	—	18	—	18	—	4	—	,,
	38	149	29	—	21	—	13	—	15	—	5	—	,,
	39	150	46	—	28	—	15	—	23	—	16	—	,,
	40	152	65	—	20	—	36	—	46	—	2	—	,,
	41	153	91	—	46	—	42	—	52	—	11	—	,,
	42	154	31	—	17	—	14	—	21	—	8	—	,,
	43	155	14	—	8	—	8	—	—	—	—	—	,,
	44	156	12	—	6	—	5	—	—	—	—	—	,,
	45	157	33	—	15	—	21	—	13	—	8	—	,,
	46	158	12	—	5	—	6	—	4	—	2	—	,,
	47	159	19	—	7	—	10	—	5	—	7	—	,,
Parent a purple hood.	48	'06, 301	—	—	90	—	—	—	—	—	69	—	'05, 309
	49	306	—	—	40	—	—	—	—	—	11	—	,,
	50	362	—	—	28	12	—	—	—	—	22	5	,,
	51	369	—	—	61	—	—	—	—	—	21	—	,,
	52	373	—	—	18	—	—	—	—	—	6	—	,,
	53	375	—	—	45	—	—	—	—	—	12	—	,,
Parent a red.	54	'06, 308	—	—	—	—	—	41	—	18	—	—	'05, 309
	55	309	—	—	—	—	—	19	—	6	—	—	,,
	56	313	—	—	—	—	—	53	—	22	—	—	,,
	57	364	—	—	—	—	—	(many)	—	(many)	—	—	,,
	58	366	—	—	—	—	—	(,,)	—	(,,)	—	—	,,
	59	367	—	—	—	—	—	(,,)	—	(,,)	—	—	,,
Parent a white.	60	'06, 311	—	—	—	—	—	—	—	—	(many)	—	'05, 309
	61	380	—	—	—	—	—	—	—	—	(,,)	—	,,
	62	381	—	—	—	—	—	—	—	—	(,,)	—	,,
	63	382	—	—	—	—	—	—	(many)	—	(,,)	—	,,
	64	386	—	—	—	—	—	—	30	17	10	—	,,

B. *Sterility of Anthers and Axil Colour.*—Evidence has been given in a previous Report (II, pp. 83 and 97), for regarding the dark axil of the Sweet Pea as dominant to the light; and in the same Report (p. 91) it was shown that the sterile condition of the anthers is recessive to the fertile.* Further, it was noticed that when light and dark axils, as well as fertile and sterile anthers, occur in the same family, the great majority of the fertile plants have a dark axil, while the light axil is associated more closely with the steriles. The details of the families are shown in Table III. Collecting together the coloured individuals (in which alone the dark axil can appear) of families heterozygous in axil and sterility, and adding in those already recorded in Report II, we obtain the following numbers:—

	From Table.	From Report II.	Total.	
Dark axil fertile	506	121	627	*637*
Dark axil sterile	22	5	27	*27*
Light axil fertile	15	2	17	*27*
Light axil sterile	175	39	214	*194*

As the last column of figures shows, we obtain a fair approximation to the recorded numbers if we suppose the gametes to be produced in series of 32, viz., 15 dark fertile, 1 dark sterile, 1 light fertile, and 15 light sterile. The closeness with which the experimental results accord with the proportions calculated upon this basis leaves little doubt but that we are here concerned with such a series.

The Wild Sweet Pea.

Through the assistance of Dr. Harmer we were enabled in 1905 to sow some seed of the wild Sicilian Sweet Pea kindly sent by Dr. Gojacono. The resulting plants were, on the whole, very like the Purple Invincible (P. I.). They were, however, smaller and of less luxuriant habit, and the colour of the wings was of a somewhat brighter blue. As in the P. I., the blue wings were not infrequently flaked with purple. Both light and dark axilled plants occurred.

One of the light axilled plants was fertilised with pollen from the white Emily Henderson (round pollen), a strain which numerous experiments have shown to be homozygous for the factors for uniform colour distribution (D)† and for the light wing (Wl), as well as for the

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* In families where fertiles and steriles come, the total numbers now stand at 1688 fertile and 541 sterile, expectation being 1672 and 557 (*cf.* Table III).

† For nomenclature, see Report III, p. 31.

Table III.

	Purple.				Red.				White.		Reference Number.
	Fertile.		Sterile.		Fertile.		Sterile.		Fertile.	Sterile.	
	dk.	lt.	dk.	lt.	dk.	lt.	dk.	lt.			
Heterozygous for axil.	32	3	—	7	8	—	1	2	10	4	'04 G. 181
	18	—	2	5	7	—	—	4	12	4	'04 F. 141
	19	—	—	7	10	—	—	4	—	—	142
	43	2	—	17	—	—	—	—	—	—	143
	23	2	—	12	—	—	—	—	13	2	144
	53	1	1	14	—	—	—	—	28	5	'05 G. 316
	—	—	—	—	50	—	1	11	41	10	317
	35	2	1	18	6	—	—	2	17	4	'05 F. 120
	—	—	—	—	20	1	1	5	6	4	'06 G. 342
	22	2	1	6	—	—	—	—	11	4	348
	—	—	—	—	57	1	3	21	22	10	349
	28	1	2	6	—	—	—	—	13	—	350
	7	2	—	5	7	2	—	2	5	4	351
	7	—	1	6	—	—	—	—	3	—	352
	—	—	—	—	22	2	1	5	4	3	353
	—	—	—	—	15	1	—	8	9	—	358
	17	—	—	5	—	—	—	3	5	2	354
Homozygous for axil.	—	50	—	19	—	—	—	—	16	5	'05 G. 315
	61	—	19	—	23	—	9	—	25	7	318
	—	81	—	12	—	17	—	7	65	20	'05 T.L. 2
	—	—	—	—	—	55	—	24	54	9	3
	—	84	—	19	—	20	—	7	71	20	5
	—	32	—	20	—	19	—	—	36	9	'06 G. 340
	—	36	—	15	—	14	—	3	40	10	360
	—	175	—	45	—	46	—	23	69	22	'07 G. 90

absence of blueness (b), of one of the colour factors (c), and of the factor for the dark axil. In other words, E. H. rd. is really a light axilled Painted Lady (P. L.) with round pollen, which lacks one of the two factors necessary for the production of colour. All the F_1 plants were of the regular P. I. type with light axils. In the F_2 generation we obtained three colour types, viz., P. I., P. L., and white, together with long and round pollens. The F_2 generation came true to the light axil. The aggregate numbers for the three F_1 plants used were as follows :—

	Observed.	Calculated.
Purple long	81	65
Purple round	1	7
Red long	7	7
Red round	17	17
White long	18	24
White round	4	8

The numbers of the round purples and of the whites are below expectation, but the figures are somewhat scanty.

The chief interest attaching to this cross lies in the light which it throws upon the constitution of the wild purple. The only recessive features which appear in the F_2 generation,* viz., red, white, and round pollen, are those which we know to have been carried into the cross by the E. H. rd. parent. The wild must, therefore, be regarded as homozygous for all the factors dominant to these.

POULTRY.

(Experiments by W. Bateson and R. C. Punnett.)

1. *Comb Characters.*

A. *The Relation of the Rose to the Single Comb.*—In our last Report (p. 13) we gave reasons for regarding the phenomena exhibited in the inheritance of the four combs, single, rose, pea, and walnut, as forming a case of dihybridism. We suggested that the allelomorphic pairs concerned are—(1) Rose (R) and absence of rose (r), and (2) Pea (P) and absence of pea (p). On this view the single comb, which makes its appearance in F_2 only in the absence of both R and P, must be looked upon as a common basis upon which these factors may be superposed. Thus every rose is a single to which the factor for roseness (R) has been added. On the removal of this factor by a suitable cross the single is revealed in F_2.

Mr. Hurst suggested that the experiment of crossing Breda × Rose might give an interesting confirmation of these views. For if rose is really single + rose, singles should appear in F_2. The Breda is a breed which has ostensibly no comb. As a matter of fact, in the cocks there are two minute papillæ standing one on each side of the middle line, which are rudiments of a comb structure. As experiment shows, the hens have the duplicity of which these papillæ are the evidence, but in examination of the heads of hens practically no comb tissue can be seen or felt.

When Breda† is crossed with single, F_1 has a large double comb

* Apart, of course, from the light axil character, in which both parents were homozygous.

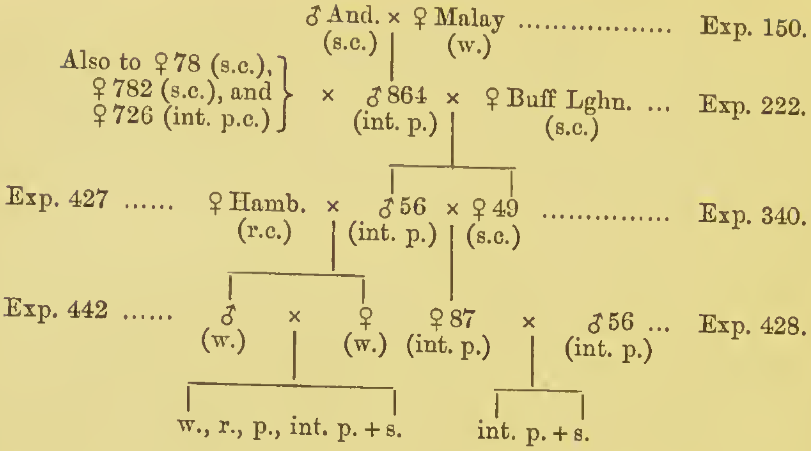
† Madame de Vries, to whom we mentioned our wish to try Bredas, very kindly put us in communication with Dr. Kerbert, of the Zoological Gardens in Amsterdam. He was good enough to interest himself in the matter, and found that Mr. Houwink, of Meppel, was willing to present us with these fowls. For this help, we desire to express our warmest thanks to Mr. Houwink and to others who have assisted us.

formed as two divaricating singles, not unlike that of the Egyptian (Rep. II, p. 113). Evidently, therefore, the Breda has a factor for duplicity which can split the single comb, but it is without the element for the single comb itself. The absence of comb in the Breda cannot be due to any factor which is actively preventing the appearance of a single comb, for if that were so, the Breda condition would be dominant.

The Breda was next crossed with a rose, and the resulting combs were all duplex roses. Two of these were bred together in 1907 and gave duplex and common roses, duplex and common singles, and Bredas. The important point is that singles appear in the F_2 generation from such a cross, and the fact of their appearance is strongly confirmatory of the view expressed above as to the relation subsisting between the rose and the single combs. To express this relation, we propose the terms *epistatic* and *hypostatic.* The factor for rose is epistatic to the factor for single, and the single factor is hypostatic to the rose.

B. *The Malay Comb.*—In Report III (p. 16) we referred to a ♀ Malay which gave all four types of comb when crossed with a single, and was presumably of the constitution RrPp. In 1906 this bird was crossed with a ♂ heterozygous in both R and P (*i.e.*, RrPp), and gave (Experiment 419) 3 singles, 3 roses, 5 peas, and 13 walnuts. We are inclined to believe that she would have given a similar result with a Malay ♂ of the constitution RrPp if we had been able to procure one to breed from, and that the rarity of rose and single combs in this breed is due rather to the rarity of birds which are heterozygous in P than to any other cause. It would appear that the great majority of Malays are homozygous for P, since of the 20 tested by us in our experiments, only four were heterozygous for this factor. The chances of heterozygotes being mated together are therefore not large, and as neither single nor rose can arise except from such a form of mating, we consider it not unlikely that the rarity of these combs results from this cause. Nevertheless we fully recognise that the question cannot be considered settled until two pure Malays, heterozygous for both R and P, have been successfully mated together.

C. *Intermediate Pea-combs.*—In our last Report (p. 16) we referred to certain types of pea-comb in which so little of the pea character was evident that in young chicks they were easily mistaken for singles. For several years we have been carrying on a series of experiments designed to throw light upon the nature of this form of comb, and the pedigree here given will make the account of these experiments less difficult to follow :—


♂ And. (s.c.) × ♀ Malay (w.) ...... Exp. 150.
Also to ♀ 78 (s.c.), ♀ 782 (s.c.), and ♀ 726 (int. p.c.)
× ♂ 864 (int. p.) × ♀ Buff Lghn. (s.c.) ... Exp. 222.
Exp. 427 ...... ♀ Hamb. (r.c.) × ♂ 56 (int. p.) × ♀ 49 (s.c.) ...... Exp. 340.
Exp. 442 ...... ♂ (w.) × ♀ (w.)
♀ 87 (int. p.) × ♂ 56 (int. p.) ... Exp. 428.
w., r., p., int. p. + s.
int. p. + s.

In 1904 a ♂ from a cross between a Malay ♀ and a ♂ Andalusian (Experiment 150), and therefore heterozygous for P, was mated with the following four hens :—

			Pea and int. p.	s.c.
Experiment 223............	♀ 726	int. p.	28	7
„ 222............	♀ 13	s.c.	17	46
„ 225............	♀ 78	„	12	18
„ 224............	♀ 782	„	9	7

In the ♂ (864) and in ♀ 726 the comb was what fanciers call a "floppy" one, hanging over on one side of the head much as in a hen Leghorn. In each case, however, it possessed distinct lateral ridges. Among the offspring of these two birds were a few low pea-combs, but the greater number were of the intermediate type. It was, however, found impossible in many cases to assign the comb of the newly-hatched chicken to either of these two forms of pea-comb with certainty. This mating gave 7 singles out of 35 chicks, a figure not far removed from expectation, which is here 9. And when mated with two s.c. ♀ ♀ in Experiments 224—5, this ♂ gave 21 P. and int. p. to 25 singles—a proportion sufficiently close to the expected equality. So far the story is clear. But when the ♂ was crossed with a Buff Leghorn ♀ (Experiment 222) he is recorded as having given 46 single and only 17 P. and int. p. instead of the equality expected. The great majority of these observations were made on hatching, and we found subsequently that it is often impossible to distinguish between the single and certain forms of intermediate pea-combs at this stage. In this very case one of the few birds reared was ♂ 56, which was registered as a single on hatching. Later he was found to have developed distinct lateral ridges, and the comb, which had started to grow with the erectness of a single, showed a distinct tendency to flop over to one side. On being mated with the single combed ♀ 49 (a sister bird), he is recorded as having given 38 s., 28 pea and intermediate pea, and 3 dubious (the last probably int. p.). These figures support the view that he was heterozygous for P., and that ♀ 49 was a pure single. From this mating (Experiment 340) was saved ♀ 87. The comb of this bird was of the form of an intermediate P. though the lateral ridges were not developed. With ♂ 56 she gave 11 pea and int. p. and 3 singles—a close approach to the expected 3 : 1 ratio (Experiment 428). In the same year (1906) ♂ 56 was tested by crossing him with a pure rose-combed Hamburgh.* The character of the offspring, 13 rose and 14 walnuts, conclusively prove him to have been heterozygous for P. In the following year two of these walnuts were bred together (Experiment 442), and, as expected, gave the usual four types of comb. Of the pea-combs some were recorded as intermediate, while others were of the regular low form of pea-comb characteristic of the pea-combed breeds. We are therefore inclined to regard the intermediate pea-combs, which show so little of the pea character, as differing from the low pea-comb in the nature of the basis upon which the pea character is imposed. That there are many types of single comb is well known, and we are inclined to consider that the nature of the hypostatic element constitutes the difference between what we have termed the intermediate and the low pea-combs.

D. *Irregular Numbers in Walnut Combs.*—In our last Report (p. 14) we drew attention to general instances in which walnut birds mated with singles had given irregular figures. Two such birds, ♂ 549 and ♂ 144, were kept for further study. In 1905 ♂ 549, mated with various s.c. ♀ ♀ (Experiments 373—4), gave 56 s., 47 r., 45 p., and 28 w., where equality is expected. The marked excess of singles and the equally marked deficiency of walnuts led us to mate him with singles in 1906 and 1907. During these two years he gave (Experiments 411, 412, 416, and 449) 31 s., 26 r., 31 p., and 36 w., expectation being 31 of each sort. He was also mated with several walnut ♀ ♀ which had previously been proved to give off equal numbers of the four types of gamete. In these experiments (Experiments 413—5 and 447—8) he gave 6 s., 25 r., 32 p., and 79 w.—expectation being 9 s., 26·5 r., 26·5 p., and 80 w. During 1906—7, therefore, this ♂ gave a regular result, and we are quite at a loss to account for the uneven figures which we obtained from him in 1905.

As already mentioned in Report III (p. 14), the walnut combed ♂ 144 in 1905 gave a normal result with 4 s.c. ♀ ♀ (Experiments 345—6). But with two white Leghorn ♀ ♀ (Experiments 347—8) he gave a very marked deficiency of roses and walnuts.

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* For this bird, we are indebted to the kindness of Mr. Fryer, of Chatteris. It is mentioned in Table IV as G. H., Golden Hamburgh.

Table IV.

For meaning of abbreviations, see Rep. III, p. 22.

1906.

Pen.	Exp. No.	Mother.	Origin (numbers refer to expts.).	Cb.	Used also in exp.	Father.	Origin (numbers refer to expts).	Cb.	Used also in exp.	Nature of mating.	Combs. S.	R.	P.	R.P.
1	394	30 31		r.p.		29		p.		R.r.P.p. × r.r.P.p.	8	11	20	19
3	395	659	267	s.	370	585	W. R.	r.	369–70	r.r.p.p. × R.R.p.p.		8		
	396	623	268	r.p.	342	"	"	"		R.r.P.p. × R.R.p.p.		12		8
4	397	390	343	p.		137	342	s.		r.r.P.p. × r.r.p.p.	9		8	
	398	632	268	r.p.	342	"	"	"		R.r.P.p. × r.r.p.p.	3	7	2	5
5	399	2 ♀ s.	W. R.	r.		184	"	p.		R.R.p.p. × r.r.P.p.		23		23
7	400	245	345	r.		228	345	s.		R.r.p.p. × r.r.p.p.	41	33		
	401	109	180	r.p.	307	"	"	"		R.r.P.p. × r.r.p.p.	3	5	2	6
8	402	3 ♀ s.	Br. L.	s.		345	347	p.		r.r.p.p. × r.r.P.p.	10		19	
10	403	532	285	r.p.	341	6	G. B.	s.	267 268 342 343 344	R.r.P.p. × r.r.p.p.	4	7	6	3
	404	658	267	s.		"	"	"		r.r.p.p. × r.r.p.p.	7			
	405	7	G.B.	"	267	"	"	"		"	14			
11	406	285	269	"	296	365	276	"	293-7	"	29			
	407	128	276	"		"	"	"		"	31			
12	408	604	211	"		91	299	"		"	23			
	409	150	299	"		"	"	"		"	23			
13	410	231	345	r.		183	345	p.		R.r.p.p. × r.r.P.p.	18	16	14	16

14	411	227	269	s.		549	233	r.p.	373–4	r.r.p.p. × R.r.P.p.	11	2	6	6
	412	571	237	"		"	"	"		"	10	17	20	18
	413	495	239	r.p.	324	"	"	"		R.r.P.p. × R.r.P.p.	2	6	11	26
	414	578	233	"	386	"	"	"		"	1	1	4	7
	415	231	202	"	302	"	"	"		"	0	12	11	31
	416	317	W.L.	s.	377	"	"	"		r.r.p.p. × R.r.P.p.	2	4	1	1
15	417	410	276	"	294	224	339	"		"	5	6	4	2
	418	186	339	r.		"	"	"		R.r.p.p. × R.r.P.p.	3	14	5	9
	419	6	Mal.	r.p.	277 334	"	"	"		R.r.P.p. × R.r.P.p.	3	3	5	13
16	420	324	236	"		432	237	s.	326–35	R.r.P.p. × r.r.p.p.	2	1	0	1
	421	465	237	s.		"	"	"		r.r.p.p. × r.r.p.p.	12			
	422	151		"	211 299	"	"	"		"	16			
	423	299	345	r.p.		"	"	"		R.r.P.p. × r.r.p.p.	13	10	13	6
17	424	339	351	"		135	299	"		"	8	8	6	9
	425	600	215	"		"	"	"		"	6	4	3	5
	426	105	299	s.		"	"	"		r.r.p.p. × r.r.p.p.	49			
21	427	167	G. H.	r.		56	222	int.p.	340–1	R.R.p.p. × r.r.P.p.		13		14
	428	87	340	int.p.		"	"	"		r.r.P.p. × r.r.P.p.	3		11	
22	429	515	237	s.		144	253	r.p.	345–8	r.r.p.p. × R.r.P.p.	8	13	8	5
	430	452	276	"		"	"	"		"	6	5	6	3
	431	895	W. L.	"		"	"	"		"	3	6	5	1
	432	315	W. L.	"		"	"	"		"	7	9	9	10
25	433	442	348	p.		435	348	p.		r.r.P.p. × r.r.P.p.	16		51	
26	434	412	377	s.		431	377	s.		r.r.p.p. × r.r.p.p.	15			
30	435.	144 279 143	350	r.		323	350	r.		R.R.p.p. × R.R.p.p.		93		
31	436	259	356	"		496	356	"		R.r.p.p. × R.r.p.p.	7	25		
32	437	426	370	"		428	370	"		"	7	19		

Table IV—*continued.*

1907.

Pen.	Exp. No.	Mother.	Origin (numbers refer to expts.).	Cb.	Used also in exp.	Father.	Origin (numbers refer to expts.).	Cb.	Used also in exp.	Nature of mating.	Combs. S.	R.	P.	R.P.
1	438	30		r.p.	394	29		p.	394	R.r.P.p. × r.r.P.p.	0	4	7	3
	439	245	345	r.	400	”		”		R.r.p.p. × r.r.P.p.	4	1	3	2
	440	151		s.	422	”		”		r.r.p.p. × r.r.P.p.	7		13	
	441	W. Wy.		r.		”		”		R.R.p.p. × r.r.P.p.		11		9
4	442	398	427	r.p.		377	427	r.p.		R.r.P.p. × R.r.P.p.	2	2	8	10
7	443	442	348	p.	433	432	237	s.	420–3	r.r.P.p. × r.r.p.p.	17		15	
	444	404	237	s.	393	”	”	”		r.r.p.p. × r.r.p.p.	17			
10	445	31		r.p.	394	226	410	”		R.r.P.p. × r.r.p.p.	5	10	8	7
	446	317	W. L.	s.	416	”	”	”		r.r.p.p. × r.r.p.p.	21			
14	447	578	233	r.p.	414	549	233	r.p.	411–6	R.r.P.p. × R.r.P.p.	2	2	2	4
	448	259	394	”		”	”	”		”	1	4	5	11
	449	317	W. L.	s.	446	”	”	”		r.r.p.p. × R.r.P.p.	8	3	4	11
17	450	30		r.p.	438	241	400	s.		R.r.P.p. × r.r.p.p.	1	3	2	0
	451	398	427	”	442	”	”	”		”	10	9	3	11
	452	442	348	p.	443	”	”	”		r.r.P.p. × r.r.p.p.	19		12	
25	453	150	299	s.		435	348	p.	433	r.r.p.p. × r.r.P.p.	17		20	
	454	176	410	r.		”	”	”		R.r.p.p. × r.r.P.p.	10	10	15	10
	455	258	394	p.		”	”	”		r.r.P.p. × r.r.P.p.	2		12	

In 1906 he was again mated with these two birds (Experiments 431—2) and gave 10 s., 15 r., 14 p., and 11 w., a fairly regular result. In all we have bred 238 birds from s.c. hens by this ♂, the numbers being 59 s., 61 r., 71 p., and 47 w.

We have noticed that where there is a tendency towards irregularity of numbers the irregularity is nearly always due to a deficiency of walnuts, and that this is frequently associated with some excess of singles. This is brought out in the total numbers for the mating of walnut with single given in Table V. Where expectation is 682 in each case there are actually 716 singles and 644 walnuts. Similarly in the mating together of walnuts of the constitution RrPp, singles are somewhat in excess of expectation (45 to 35), while walnuts are rather below it (279 to 312). These irregularities in the expected distribution of the various types seem to point to the operation in certain cases of some definite disturbance, but we cannot at present venture upon any surmise as to its nature.

E. *Summary of Comb Results.*—Our experiments upon the inheritance of the walnut comb and of its components, the rose, the pea, and the single, are now concluded, and we may briefly recapitulate the explanation which we have already given in our third Report (p. 12). The case is one of simple dihybridism in which both the factors concerned affect the same structure, the comb. These factors are roseness (R) which is allelomorphic to its absence (r), and peaness (P), which is also allelomorphic to its absence (p). A walnut comb is one in which both R and P are present, and such a comb may be either homozygous or heterozygous for one or both of these factors. Judged by the criterion of gametic output, four kinds of walnut comb, and only four, are possible, viz., RRPP, RRPp, RrPP, and RrPp. These four kinds we have met with over and over again, and we have met with no others. So also there are two kinds of rose and two kinds of pea, viz., those homozygous and those heterozygous for the respective dominant factor which they contain. All single combs, whatever their origin, are of the constitution rrpp, and consequently breed true to that character.

As the results which have led us to these conclusions are scattered over four Reports and involve the consideration of over 12,500 birds, we have collected them together in Table V :—

Table V.

Visible nature of mating.	Constitutional nature of mating.	References to Reports and No. of experiment.	Result.			
			S.	R.	P.	R.P.
Rose × Rose	R.R.p.p. × R.R.p.p.	III, 280, 290, 350, 356, 369; IV, 435	—	270 [all]	—	—
	R.R.p.p. × R.r.p.p.	II, 121, 157	—	31 [all]	—	—
	R.r.p.p. × R.r.p.p.	I, 37–40, 85; II, 156; IV, 436–7	235 *[232·5]*	695 *[697·5]*	—	—
Rose × Single	R.R.p.p. × r.r p.p.	I, 24-33; II, 95–7, 103, 113, 122, 136, 151, 184; III, 200, 273, 370; IV, 395	1	484 [all]	—	—
	R.r.p.p. × r.r.p.p.	I, 41, 70-8, 87; II, 100, 102, 112, 113*a*, 114, 115, 118, 139, 147, 149, 192; III, 246, 263-6, 274, 330; IV, 400	703 *[698·5]*	694 *[698·5]*	—	—
Pea × Pea	r.r.P.P. × r.r.P.P.	III, 281	—	—	21 [all]	—
	r.r.P.P. × r.r.P.p.	II, 110, 128	—	—	31 [all]	—
	r.r.P.p. × r.r.P.p.	I, 34–6, 80–1; II, 106, 125; III, 228, 229; IV, 433, 455	210 *[194·25]*	—	567 *[582·75]*	—
Pea × Single	r.r.P.P. × r.r.p.p.	I, 1–23; II, 126, 127; III, 250, 282, 292, 301, 384	5	—	660 [all]	—
	r.r.P.p. × r.r.p.p.	I, 42–62, 82; II, 89, 90, 98, 107–9, 130, 140–1, 145, 148, 154–5, 160; III, 230–1, 368; IV, 397, 402, 443, 452–3	514 *[502]*	—	490 *[502]*	—
Rose × Pea	R.R.p.p. × r.r.P.P.	II, 93, 94, 152, 186	—	—	—	49 [all]
	R.R.p.p. × r.r.P.p.	II, 185, 187; IV, 399, 427, 441	—	47 *[46·5]*	—	46 *[46·5]*

	R.r.p.p. × r.r.P.P.	II, 178, 179, 180	—	—	71 [*77*]	83 [*77*]
	R.r.p.p. × r.r.P.p.	II, 111 ; IV, 410, 439, 454	34 [*32·75*]	32 [*32·75*]	35 [*32·75*]	30 [*32·75*]
Walnut × Walnut	R.r.P.p. × R.r.P.p.	III, p. 15 ; IV, 413–5, 419, 447–8, 442	45 [*35*]	99 [*104*]	132 [*104*]	279 [*312*]
Walnut × Rose	R.r.P.P. × R.r.p.p.	III, 198	—	—	6 [*6·5*]	20 [*19·5*]
	R.r.P.p. × R.r.p.p.	IV, 418	3 [*3·9*]	14 [*11·6*]	5 [*3·9*]	9 [*11·6*]
Walnut × Pea...............	R.r.P.p. × r.r.P.p.	IV, 394, 438	8 [*9*]	15 [*9*]	27 [*27*]	22 [*27*]
Walnut × Single............	R.R.P.p. × r.r.p.p.	III, p. 14	—	140 [*144·5*]	—	149 [*144·5*]
	R.r.P.P. × r.r.p.p.	III, p. 13 ; II, 150, 161	—	—	309 [*304*]	299 [*304*]
	R.r.P.p. × r.r.p.p.	II, pp. 109–110 ; III, p. 14 ; IV, 398, 401, 403, 411–2, 416, 417, 420, 423, 424–5, 445, 450–1, 429–432	716 [*682·2*]	705 [*682·2*]	664 [*682·2*]	644 [*682·2*]
	R.R.P.P. × r.r.p.p.	III, p. 13.	—	—	—	216 [all]
Single × Single	r.r.p.p. × r.r.p.p.	II, 91, 92, 99, 101, 104, 116–7, 119, 120, 129, 131–3, 138, 146, 149, 157*a*, 158, 183 ; III, 209–211, 237, 247–8, 269, 270, 276, 293–6, 299, 367, 375–7 ; IV, 404–9, 421–2, 426, 434, 444, 446	1937 [all]	—	—	—

The expectations are given in square brackets.

For the various types of mating shown in Table V the expectation based on theory has been added in brackets below the experimental figures in each case. References to the original records used in compiling the table are given throughout.

Dubious and Unconformable Results.—In previous reports 23 birds were recorded at different times as having combs not at once referable to one of the four types studied in these experiments. These birds are not represented in the above summary. The sources of uncertainty were various and in several cases the doubt arose merely through unfamiliarity with the material. These in the light of fuller experience could, without doubt, have been classified easily. The only cases in which genuine doubt arises are those intermediate singles of which a full account is given on p. 19. In the families where these occur the classification is uncertain and mistakes have occurred. Besides these, certain actual unexpected results are recorded as shown in the summary, Table V. Five birds came with single combs in Experiments 13, 21, 22, and 22A where only pea-combs are expected. These may, perhaps, have been of the intermediate pea class. One single comb occurred also in Experiment 26, where roses only are expected.

2. *White Plumage.*

In the last Report (p. 18), it was shown that there are two distinct classes of white fowls: (*a*) those in which white is dominant to colour, and (*b*) those in which the white is recessive to colour. The recessive whites are of at least three kinds, viz.:—

(1) *The White Birds which have arisen in the course of our Experiments* (Rep. III, pp. 19—20).—These birds often have one or more coloured ticks in their plumage, and we formerly regarded these specks of colour as characteristic of the recessive white. This suggestion is, however, incorrect, as we have now had birds of this white strain quite devoid of colour and indistinguishable from dominant whites, except by breeding tests. The down of such birds is also without colour. The recessive whites of this type we shall speak of as R-whites.

(2) *The White of the Silky Fowl.*—Such birds, when adult, are, or may be, perfectly white in plumage. The down of the newly-hatched chicks, however, often contains some buff, especially on the sides of the head, on the body in the position of the lateral *light* stripes of a brown chicken, and on the rump. The amount of buff varies, but we are not sure that the Silkies of our strain ever hatch without any colour; for, at the time they were hatched, this point had not occurred to us.

(3) *The White of the Rose-comb Bantams.*—These always have a few, generally minute, ticks in the adult plumage, though, in other respects, fully white birds. In the down their chicks are *pale bluish.*

Each of these types of white behaves as a simple recessive to colour, but when the R-white is crossed with the Silky white the offspring *are all fully coloured*, with plumage somewhat resembling that of a poor black-red.

This phenomenon is superficially comparable with that seen in Sweet Peas and Stocks where two albinos are crossed with production of a coloured F_1. In the fowls, of course, we are not dealing with albinos at all. The birds all have pigmented eyes, and in the case of the Silky the buff in the down is already an indication of the presence of some pigmentation. As the experiment shows, however, the R-white contains some factor which is complementary to that present in the Silky, and is needed to produce the fully coloured type of plumage. The two complementary factors may be called X and Y. Each of these factors must be regarded as allelomorphic to its absence (*cf.* Rep. III, p. 3); consequently, one parent, say the R-white, may be represented as xxYY, and the Silky as XXyy, and thus the cross of either Silky or R-white with such breeds gives coloured F_1 and 3 coloureds to 1 white in F_2.

The Silky crossed with the white Rose-comb gives whites only in F_1, and hence it is likely that of the two complementary factors, one only is present and common to both these types.

The dominant white we regard as containing an additional factor, D, whose action is to prevent or diminish the production of colour by the factors X and Y.

The details of our experiments are as follows :—

A. *R-Whites.*—In Report III (pp. 19–20), will be found the pedigree of a white ♂ 144 which gave only coloured offspring* when crossed with various coloured birds. Two pairs of his offspring out of a Brown Leghorn ♀ were mated together in 1906. Between them they gave 105 coloured and 33 whites.† The close approximation to the 3 : 1 ratio shows that the white in this case behaves as a simple recessive to colour. Many of these extracted whites were reared, and form the stock of which we have made use in our subsequent experiments.

B. *Silky-White.*—The following evidence collected during the past few years shows that the white plumage of this breed is recessive to colour :—‡

(1) 7 Silkies (4 ♂ ♂ and 3 ♀ ♀) crossed with pure coloured birds gave 220 chicks all coloured.

(2) F_1 birds from Silky × Brown Leghorn crosses bred together have given 156 coloured and 44 light, expectation being 150 and 50.

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* See also p. 34.

† These families are dealt with in connection with colour on p. 34.

‡ Davenport ('Publ. Carnegie Inst. Washington,' No. 52) crossed a Silky ♂ with 4 coloured frizzled ♀ ♀, and obtained 7 white and 25 dark birds. This result is explicable on the supposition that at least one of the ♀ ♀ was heterozygous for the factor C.

(3) F_1 birds crossed with pure Silky gave 98 coloured and 79 light birds, expectation being 88·5 of each.

C. *Silky-White* × *R-White.*—We have made this cross in six different cases. All the 113 birds produced were fully coloured. Some of these birds have been kept in order to breed from in 1908. From the analogy of the Sweet Pea case (*cf.* Rep. III, p. 3), we look for coloured and whites in the ratio 9 : 7.

[*Note added July* 19, 1908. From two pens of such F_1 birds mated this year we have had 203 chicks. Of these, 116 were coloured and 87 were light, with or without buff—expectation being 114 coloured and 89 light.]

D. *Dominant White* × *R-White.*—In 1905, our original R-white ♂ was crossed with two White Leghorn hens (Experiments 347, 348) in which white was dominant to colour. The resulting offspring, 38 in number, were all white, as were 50 chicks similarly bred in the following year (Experiments 431, 432). Three of these F_1 birds were kept and their constitution tested by crossing them with: (1) pure coloured birds, (2) recessive whites, and (3) one another, and the three types of experiment may be considered in this order.

(1) The F_1 birds must, on our hypothesis, be heterozygous for D, and should, when crossed with pure coloured birds, give equal numbers of coloured and whites. Actually they gave 43 whites and 56 coloured.

(2) Two of the F_1 birds were further tested by mating them with recessive whites (Experiments 452, 454). On the assumption that the constitution of the dominant white was DDYYXX, and of the recessive white ddYYxx, that of the F_1 bird should be DdYYXx. Such birds would produce equal numbers of gametes of four kinds, viz., DYX, DYx, dYX, and dYx. The gametes of the recessive white are all dYx. The F_1 bird mated with a recessive white should, consequently, give whites and coloured in the proportion 3 : 1. Actually, two F_1 birds so mated gave 62 whites and 15 coloured, expectation demanding 58 of the former and 19 of the latter.

(3) Two F_1 birds mated together (Experiment 433) gave 63 white and 4 coloured. If, as supposed, the constitution of the F_1 bird is DdYYXx, we should get, in F_2, whites and coloureds in the proportion of 13 : 3. The accompanying scheme renders it clear how this is brought about. The proportion of coloured birds found by experiment is distinctly lower than that which is expected. This may be merely the result of chance or it may be due to the fact that the F_1s are heterozygous for Y. That the F_1 birds are heterozygous for D is shown by the result of the cross with a pure-coloured, and the result of mating with an R-white proves them to be heterozygous for X. But neither of these tests can distinguish a bird which is heterozygous for Y from

one which is homozygous. Two birds of the constitution DdYyXx would, when mated together, give whites and coloured in the proportion of 55 : 9—a proportion which is nearer to the result which we have obtained from our only experiment of this nature. Moreover, it is not unlikely that White Leghorns are sometimes heterozygous for Y or

DYX DYX wh.	DYX DYx wh.	DYX dYX wh.	DYX dYx wh.
DYx DYX wh.	DYx DYx wh.	DYx dYX wh.	DYx dYx wh.
dYX DYX wh.	dYX DYx wh.	dYX dYX col.	dYX dYx col.
dYx DYX wh.	dYx DYx wh.	dYx dYX col.	dYx dYx wh.

even homozygous for its absence; for we know that the breed has been crossed with white Malays for size, and the white Malay is a recessive white.* The point could be tested by crossing with the Silky white, when birds homozygous in Y would give equal numbers of whites and coloureds, while birds heterozygous in Y would give whites and coloured in the ratio 3 : 1. The F_1 birds used in the above experiments are no longer available, but we bred others in 1907, and we hope to test them fully during the present year (1908). For the present we are inclined to consider the dominant white as homozygous for Y and X, and to regard the small number of coloureds which appeared in Experiment 433 as a chance result.

We may add that the total number of coloureds and whites which have appeared in the various matings into which the F_1 birds entered is very close to expectation. Out of 243 birds, 168 were white and 75 coloured, where 162 white and 81 coloured were expected.† The various experimental results as to the inheritance of white plumage with which we have been dealing are summarised in Table VI. The figures in italics denote the expected figures in each case.

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[*] For it is known to occur in the breeding of coloured Malays.

[†] The expectation here, of course, is not a single one, but is arrived at by combining the various expectations concerned.

Table VI.

Cross.	Nature of mating.	Result.		Expectation.	
		white.	colour.	white.	colour.
R-white × colour …………	ddYYxx × ddYYXX	—	149	—	all
F_1 ex R-white × colour with similar bird	ddYYXx × ddYYXx	33	105	*34·5*	*103·5*
Silky-white × colour ……	ddyyXX × ddYYXX	—	220	—	all
F_1 ex Silky-white × colour with similar bird	ddYyXX × ddYyXX	44	156	*50*	*150*
F_1 ex Silky-white × colour with pure Silky	ddYyXX × ddyyXX	79	98	*88·5*	*88·5*
Silky-white × R-white ……	ddyyXX × ddYYxx	—	113	—	all
D-white × R-white ………	DDYYXX × ddYYxx	88	—	all	—
F_1 ex D-white × R-white with similar bird	DdYYXx × DdYYXx	63	4	*54·5*	*12·5*
[or see p. 30…	DdYyXx × DdYyXx	63	4	*58*	*9*]
F_1 ex D-white × R-white with pure coloured	DdYYXx × ddYYXX	43	56	*49·5*	*49·5*
F_1 ex D-white × R-white with R-white	DdYYXx × ddYYxx	62	15	*58*	*19*

3. *Rose-comb Bantams.*

In our last Report (p. 18) we showed that in the Rose-comb bantam black plumage was dominant over white. During 1906, 3 F_1 ♀ ♀, mated with an F_1 ♂, produced 94 chicks (Experiment 435), of which 70 were black and 24 were light, a close approximation to the expected ratio 3 : 1. The recessive nature of this white was further confirmed by crossing a white Rose-comb ♂ with a brown-breasted Game bantam. Two of the resulting F_1 birds, in colour not very dissimilar to the brown-breasted breed, produced 6 light chicks out of a total of 26 (Experiment 437).

We have also carried out a few experiments with the idea of discovering the relation which the white of the Rose-comb bears to that of the R-white and of the Silky.

The cross Rose-comb white × Silky white was made three times, and gave in all 84 whites. The F_2 generation bred from such birds differed a good deal in their down colour. Some resembled the Silky white, with or without a little buff; others were of the pale smoky blue characteristic of the pure Rose-comb; others, again, were of a darker, smoky tint, and not infrequently developed into adults with a distinct dinginess in hackle and mantle. We have not attempted, however, to follow up these differences. The F_1 birds crossed back with the Silky gave 21 light chicks, and with the Rose-comb gave 26 light chicks. No really coloured bird came in any of the matings from this cross, and we are probably justified in regarding the Silky and the Rose-comb as owing their whiteness to the absence of the same factor.

If this is so, the Rose-comb should give only coloured offspring when crossed with the R-white. Disparity of size offers an insuperable obstacle to the direct cross, and we have only been able to make it indirectly by mating the F_1 ♀ ex Rose-comb × Silky with a ♂ R-white. The mating gave 28 birds, all fully coloured, from which we may infer that the Rose-comb white when crossed with the R-white behaves as the Silky white in giving only coloured birds.

4. *Brown Down Colour.*

In the account of our experiments with Game Bantams we brought forward evidence to show that the pale brown down colour is recessive to the brown striped (Rep. III, p. 21). This conclusion has been confirmed by certain experiments already referred to in connection with the inheritance of recessive white (p. 29). A white ♂ was crossed with a Brown Leghorn ♀; all the offspring were brown striped in the down, and subsequently developed into fully coloured birds. Two pairs of these F_1 birds were bred together, and each gave chicks of three different down colours, viz., brown striped, pale brown, and white. The proportions are shown in the accompanying table :—

	Brown striped.	Pale brown.	White.
Experiment 400	41	15	18
" 410	35	14	15
Total	76	29	33
Expectation	*77·6* [9]	*25·9* [3]	*34·5* [4]

The ratio is obviously a 9 : 3 : 4 ratio, and the allelomorphic pairs concerned are: (1) presence and absence of colour, and (2) presence and absence of brown stripe. The pale brown is recessive to the brown stripe. An interesting point in connection with this experiment is that both brown striped and pale brown chicks developed into birds practically identical as regards the colour of the plumage.* We are dealing here with a pair of characters which are perfectly distinct in early life but cannot be distinguished later on except by breeding tests.

5. *Andalusians and Bredas.*

A few more chicks were obtained in 1906 from the mating of a black Andalusian ♂ with a blue ♀ (Experiment 407). Of the 33 offspring 16 were blue and 17 were black, expectation being, of course, equality (*cf.* Rep. III, p. 20).

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* Compare the case of Indian Game, Rep. I, p. 88.

In 1906 we obtained from Mr. Houwink, a well-known breeder at Meppel, in Holland, two pairs of Breda fowls, viz., a pair of blacks and a pair of blues. The blacks bred true, giving 33 blacks. The blues, however, gave 8 blacks, 14 blues, and 5 chicks with the very pale blue down characteristic of white splashed Andalusians. Two of these were reared and developed into typical splashed whites. In respect of colour, therefore, the Bredas are to be classed with the Andalusians, and this is confirmed by the fact that we obtained four blues on crossing a splashed white Andalusian ♀ with the black Breda ♂. Further experiments of a similar nature have been carried out by Dr. R. N. Salaman, of Barley, who bred a blue Breda ♂ with blue Andalusian ♀ ♀ and obtained blacks, blues, and splashed whites nearly in the expected ratio 1 : 2 : 1.

6. *Silky Plumage.*

During the past two years this breed has played a large part in our experiments. The work has been concerned primarily with the inheritance of the peculiar pigmentation of the skin and tissues found in these fowls, though we have incidentally been able to confirm Davenport's view* of the recessive nature of the "silky" plumage. From the cross silky × normal plumage we have so far obtained in F_2 77 normal and 22 silky plumaged—expectation being 74 : 25. Again, on crossing the F_1 bird with the Silky (three families) we obtained 25 with normal and 28 with Silky plumage, a close approach to the expected equality.

7. *Mottled Plumage.*

We have already drawn attention to the fact that the white ♂ 144 which formed the starting point of our experiments on the R-white (p. 29) gave only coloured chicks when crossed with coloured hens. A number of his offspring from a Brown Leghorn hen (♀ 465) were reared to maturity. The down colour of all these chicks was brown striped like that of the pure Leghorn, but as they grew up they exhibited two distinct types of plumage. In one type the birds were all fully coloured, while in the other the plumage contained much white. In the latter the individual feathers were barred with colour, though the barring was much blurred and gave the birds their characteristic mottled appearance. We have been unable to carry out any extensive experiments with this mottled character, but for the following reasons we feel little doubt that it behaves as a simple dominant to the fully coloured.

(1) Out of 20 F_1 birds from the Brown Leghorn which were reared

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* Davenport, C. B., "Inheritance in Poultry," 'Publ. Carnegie Inst. Washington,' No. 52, 1906.

to maturity 11 were fully coloured and 9 were mottled. This is close to the equality demanded on the assumption that the ♂ was heterozygous for this character.

(2) Seven fully coloured F_1 birds bred among themselves (Experiments 400, 410, etc.), or with other fully coloured birds, gave no mottled young.

We may add that the ♂ 144, when crossed with a black Andalusian hen (Experiment 346), gave fully coloured blacks and mottled blacks. Dr. Salaman kindly bred from a pair of the fully coloured birds and obtained no mottled birds in the F_2 generation—a result which confirms our own experience of the Brown Leghorn cross.

STOCKS.

(Experiments by E. R. Saunders and H. B. Killby.)

Surface Character and Flower Colour. Summary and Corrigendum.

In the last Report (p. 38), an attempt was made to formulate a scheme which would bring into line the complex, and, in some cases, apparently contradictory results as regards surface character and flower colour, which had been observed in certain unions between Stocks of the following strains:—Glabrous (wallflower-leaved), Ten-week Stocks of various colours, red and white hoary Brompton Stocks, and the purple and white forms of *incana*. It was pointed out that as regards flower colour the results are explicable on the following assumptions: (1) that the sap is coloured red when two factors (denoted by the letters C and R) are both present; (2) that in the absence of either, or both, the sap is uncoloured; (3) that the presence of a third factor (B), in addition to C and R, turns the red sap blue, but that in the absence of C or R, the presence of B cannot be detected merely by inspection. In certain forms other factors in addition to these three may be present, causing either dilution of the sap colour (as, *e.g.*, in pale purple), or the appearance of less pure shades as, *e.g.*, the production of copper and plum instead of full red and purple.

As regards plastid colour (in the sap-coloured forms most easily seen in the centre or "eye" of the flower), the relation of uncoloured (white) to coloured (cream) plastids appears to be that of dominant to recessive, if a certain marked deficiency of creams in F_2, observed in some cases, should prove attributable to accidental irregularity; if, on the other hand, this deficiency should prove real, some less simple relation must evidently exist (see Rep. III, pp. 39 and 50, Table III, cases 24, 29, etc.).

In the case of surface character it was suggested that, similarly as in the case of sap colour, the dominant condition—hoariness—is due to the presence of two factors (H and K), the recessive condition—glabrousness—to the absence of either, or both, but that the flower colour and surface character are so inter-related that the outward manifestation of the presence of H and K only occurs if C and R are present in conjunction with these two factors, *i.e.*, only in sap-coloured individuals. Brompton Stocks might, however, prove an exception to this kind of zygotic coupling.

Since the publication of Report III, it has been pointed out to us by Mr. Doncaster that the assumption of two hoariness factors, H, K, is unnecessary, and that the occurrence of one alone is sufficient to account for the known facts. The double factor hypothesis, which at an earlier stage of the work appeared to offer the simplest solution of the facts, was, by an oversight, unfortunately retained after another explanation of the complications it was invoked to explain rendered it unnecessary.* This simplification is correctly represented if H is omitted from the formulæ and diagrams given in Report III. The composition of the glabrous Ten-week strains can, therefore, be stated thus:—

Glabrous white	CrK
,, cream	cRK
,, sap colours	CRk

Doubling.

During the past two seasons, considerable additional knowledge has been obtained regarding the circumstances under which doubles may be expected to occur, or, on the other hand, to be altogether absent. The evidence obtained from a large number of observations renders it scarcely doubtful that, contrary to the belief still widely held among growers, the double character is inherited in a definite and regular manner, and independently of external conditions.

The experiments recorded in Reports II and III had already shown that, in most of the glabrous Ten-week strains, *e.g.*, white, Princess May (a cream), flesh, copper, and various purple shades, the singles are of two kinds: (1) those which on self-fertilisation yield only singles; and (2) those which, similarly treated, give a mixture of singles and doubles, the doubles being usually in distinct excess of the singles. This has also been found to hold in the red and white English Brompton Stocks, and is probably true also of the East Lothian (Intermediate) strains. It was found that, in the case of the Ten-week strains mentioned above, seed obtained commercially and stated to yield a certain proportion of doubles could be relied upon to give the expected mixture, but that the singles so obtained would probably include *both* kinds of individuals, some again throwing doubles and others not. Whether such mixture commonly occurs in similar samples of thc Brompton and East Lothian strains the number of plants tested is as yet too small to determine.

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* Attention has already been drawn to this correction in the Royal Horticultural Society's 'Report of the Conference on Genetics,' 1906, p. 147; see also Bateson, 'Progressus Rei Bot.,' vol. 1, p. 391.

The results of the present experiments go to show that once an individual has been identified as belonging to the sporting or to the non-sporting class, it becomes possible to predict the behaviour of its descendants when they in turn are self-fertilised. From a non-sporting individual only non-sporting offspring are obtained; whether self-fertilised or bred *inter se*, such offspring appear incapable of throwing doubles. Conversely, singles derived from an individual belonging to the sporting group have, so far as experiment has yet gone, proved themselves to be also all of the sporting class, giving again both singles and doubles. It is, nevertheless, just possible that a small percentage of singles, offspring of double-throwing singles, may be pure singles, though none have yet been found. Such plants, if they exist, must in any case be rare, but the possibility of their existence must still be borne in mind.

Two of the Ten-week strains, however, differ from those enumerated above in that in each case the race *as a whole* appears to be ever-sporting: 77 individuals were tested in the one case and 33 in the other, and not one was found to breed true to singleness. These two strains are red (crimson) and sulphur-white. The latter race is also remarkable for its behaviour as regards plastid colour. It has been known to growers for at least fifty years, and is usually described as yielding a mixture of singles and doubles, the singles being white and the doubles cream. This statement has been found to be correct so far as the singles are concerned. Among the doubles, however, though the great majority are cream, a small percentage of whites are constantly found to occur. It may well be that in the case of these two races the original seed happened to have been collected exclusively from sporting individuals, and the aim of the gardener to obtain as many doubles as possible has tended to keep the supply, once obtained, from admixture with seed from true-breeding singles. On the other hand, it seems not improbable that the varying percentage of doubles quoted for different strains (from 30 to 80 per cent., but usually about 60 or 70 per cent.) is largely, perhaps wholly, due to the greater or lesser admixture of seed from singles of the non-sporting class, such admixture being very likely to occur where plants are grown on a large scale and harvested in bulk. The same explanation may possibly account for another fact hitherto unexplained. In a treatise advocating a new method for the successful culture of Stocks and Wallflowers, E. Chaté, a French horticulturist, remarks, in passing, that one cause of the decline in the culture of these plants among French gardeners is no doubt disappointment that the 60 or 70 per cent. of doubles obtained in the first year from German grown seed becomes diminished after a few years to 10 or 15 per cent.* If, as in our experience appears frequently to be the case, the seed obtained by Chaté was mixed, having been harvested from pure-breeding singles as well as from sporting singles, and if it be assumed that all the singles are on the average equally productive, then the proportion of the crop represented by pure-breeding singles will tend to increase in successive years, that of the sporting singles to diminish, since a large proportion of the progeny of the latter plants will be double and therefore infertile. Consequently the proportion of doubles in each successive generation must necessarily diminish, unless this effect is in any way counteracted by selection.

In the case of crosses between the various strains mentioned above, the results fully confirm the view expressed in Report III (p. 45), that doubles are only found to occur in the F_1 generation when *both* the parents throw doubles on self-fertilisation. If *only one* of the parents is found to yield doubles when self-fertilised, the F_1 generation will consist entirely of singles.

The further evidence upon which this statement is based is given in Tables I, II, and III. It will there be seen that from 79 matings between various strains, where one parent was known to be throwing doubles and the other not, 1250 F_1 plants were raised, all of which were single (Table I). Whereas the F_1 families obtained from 29 unions, where both individuals were known to be capable of throwing doubles, all showed a mixture of singles and doubles (Table II). In no case were doubles obtained from matings between individuals giving only singles when self-fertilised (Table III).

The consistency of these results, obtained from a considerable number of different strains, and the agreement between them and Mendelian expectation, according as the breeding is with heterozygous or homozygous forms, point strongly to the conclusion that the double character is inherited in accordance with Mendelian principles.

The evidence from the F_2 generation brings out two remarkable features which are not exactly paralleled by any phenomenon of inheritance hitherto observed.

(1) Though F_1 bred between pure singles and double-throwing singles is always single, there is a distinction between reciprocal crosses. For when a pure single is used as ♀ and is pollinated from a plant throwing doubles, *all* the F_1 plants throw doubles in F_2. But when the reciprocal cross is made, *some* of the F_1 plants breed true to singleness while others throw doubles.

(2) A similar difference between reciprocals occurs in regard to the

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* 'Cult. prat. des Giroflées' (N.D.), p. iii.

plastid character in the case of the sulphur-white strain. As stated above (p. 37), this is a strain of white singles throwing doubles which, a small percentage excepted, are cream.* The result in certain crosses, where this race is used as the male parent, indicates that *all* the pollen grains of the sulphur-white carry the cream character; whereas the results obtained when the same form is used as the female show that among the ovules *some* carry the cream character and some the white (see note, p. 5).

There are further complications showing that in some unknown way an interdependence exists between doubleness and the character of the plastids, but these have not yet been studied on a sufficient scale.

These two facts are a clear indication that the composition of the ovules may differ from that of the pollen grains in the same plant.

Table I.—Showing that the F_1 generation from matings where one parent is throwing doubles, and the other not, *is all single.*

A strain which throws doubles on self-fertilisation is described as a "d" strain, e which does not as a "no-d" strain. In Experiments 1—14 the seed parent is rowing doubles and the pollen parent not; in Experiments 15—20 the reverse is e case.

No. of xpt.	Parents.		No. of matings.	F_1.	
				Single.	Double.
1	No-d glabrous cream	× d hoary white (East Lothian)	3	75	0
2	,,	× d glabrous white	2	35	0
3	,,	× d hoary red (Brompton)	2	23	0
4	,,	× d glabrous red	3	35	0
5	,,	× d glabrous sulphur-white	7	76	0
6	,,	× d glabrous azure	2	43	0
7	,,	× d glabrous light purple	3	69	0
8	No-d glabrous white	× d hoary white (East Lothian)	1	2	0
9	,,	× d glabrous cream (Princess May)	3	35	0
10	,,	× d glabrous red	4	53	0
11	,,	× d glabrous sulphur-white	17	289	0
12	No-d glabrous flesh	× d hoary white (East Lothian)	1	19	0
13	,,	× d glabrous sulphur-white	9	151	0
14	,,	× d glabrous light purple	1	9	0
15	d glabrous cream (Princess May)	× no-d glabrous white	2	35	0
16	d glabrous red	× ,,	2	26	0
17	d glabrous sulphur-white	× no-d hoary red (Brompton)	4	57	0
18	,,	× no-d glabrous flesh	5	102	0
19	,,	× no-d glabrous white	3	44	0
20	,,	× no-d hoary white (*incana*)	5	72	0
			79	1250	0

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* The occasional white double appearing in this strain points to some further complexity which the data at present available are insufficient to explain.

Table II.—Showing that the F_1 generation from matings where both parents are throwing doubles *consists of a mixture of singles and doubles.*

No. of expt.	Parents.	No. of matings.	F_1.	
			Single.	Double.
1	d glabrous cream (Princess May) × d hoary white (East Lothian) ...	1	13	13
2	” ” × d glabrous white	2	2	6
3	” ” × d glabrous red	2	5	15
4	” ” × d glabrous sulphur-white	4	21	35
5	d glabrous red × d glabrous cream (Princess May)	3	14	28
6	d glabrous sulphur-white × d hoary white (East Lothian) ...	7	87	121
7	” × d glabrous red	4	15	21
8	” × d glabrous white	1	7	8
9	” × d glabrous azure	3	35	44
10	” × d glabrous light purple	2	2	23
		29	201	314

Table III.—Showing *the absence of doubles* in F_1 when both parents are pure-breeding singles.

No. of expt.	Parents.	No. of matings.	F_1.	
			Single.	Double.
1	No-d glabrous cream × no-d glabrous white	7	99	0
2	No-d glabrous white × no-d glabrous cream	1	10	0
3	” × no-d glabrous white	3	64	0
4	No-d glabrous flesh × no-d glabrous cream	2	55	0
5	No-d glabrous cream × no-d glabrous flesh	1	18	0
		14	246	0

The pollen grains of the ever-sporting race are all, or nearly all, capable of transmitting doubleness, while many of the ovules are carrying singleness. Similarly the pollen grains of the sulphur-white are all, or nearly all, transmitting the cream colour, whereas among the ovules many carry whiteness.

The nature and origin of the distinction between the two classes of ovules cannot be settled without a wide statistical basis of fact, but it is evident that a clue to the solution of the problem presented by these ever-sporting strains is provided by the distinction between reciprocals.

A PRELIMINARY ACCOUNT OF THE INHERITANCE OF COAT-COLOUR IN MICE.

By Florence M. Durham, Lecturer of Newnham College.

(Communicated by W. Bateson, F.R.S.)

During the past five years I have made a series of breeding experiments to determine the heredity of colour in mice.

As regards two important sections of the subject, namely, the nature and genetic behaviour of yellow mice, and the constitution of mice which have coloured coats and pink eyes, the experiments are as yet incomplete. The inquiry into these subjects is being continued, but as in some other respects the work is now complete, I submit a brief statement of the results.

My work has been largely confirmatory of what has been already stated by others. In addition, some new points have been made out. The relation of the dense to the dilute colours has been studied on a considerable scale. In regard to the pied varieties, the existence of a dominant pied condition has been demonstrated. The relation of the pigmentation of the eye to that of the coat has been investigated and in part elucidated.

On inspection, the colours of mice are seen to be very various, and examination shows that the different appearances are due to:—

(1) The nature of the pigment or pigments present.
(2) The density with which the pigment or pigments may occur.
(3) The pattern of their distribution in the hairs.
(4) The development of more or less white.

The allelomorphs to which these appearances are due may be represented thus:—

G. g. Presence and absence of the factor which gives the "agouti" or "grey" pattern in the hairs.

B. b. Presence and absence of the black determiner.

C. c. Presence and absence of colour.

If C is present without G or B, the colour is chocolate. From the analogy of other cases (fowls and various plants) it is possible that this colour is itself the product of two factors, but hitherto it has not been resolved. All albino mice, therefore, are to be represented as those from which C, *i.e.*, the colour chocolate is absent.

The above factors give the following combinations:—

CGB	Grey or agouti
CgB	Black
CGb	Cinnamon agouti
Cgb	Chocolate

D and d represent the presence and absence of a factor which causes the dense deposit of the pigments. CgBD is black; CgBd is blue; CgbD is chocolate; Cgbd is dilute chocolate, or "silver-fawn," as it is called by the fanciers.

When, as will be shown later, the pied condition is dominant, there is evidently another factor P present, which inhibits colour in varying degrees, whereas the recessive pied conditions are due to the absence of S, self-colour.

As described by Bateson (1), though the notation here indicated must be employed in calculating the various expectations, it is possible that the dilution states and the recessive pied states may be caused by subtraction stages of the corresponding dominant factors for dense deposition and self-colour.

Cuénot (2) originally suggested that G should be taken as allelomorphic to B. In the Report to the Evolution Committee, III, p. 7, it was pointed out that this was probably incorrect, and that by crossing agouti with chocolate a test of the correctness of the scheme, here propounded, could be obtained. If G and B were allelomorphic not to each other, but to g and b, their absences respectively, then black should appear in F_2. I have made this experiment, getting in F_2, 22 ag., 6 cinn. ag., 5 black, 3 chocolate, where expectation gives 20·5 ag., 6·75 cinn. ag., 6·75 black, 2·25 chocolate. Cuénot has similarly bred 41 ag., 15 cinn. ag., 15 black, 5 chocolate (expectation being 42·75 ag., 14·25 cinn. ag., 14·25 black, and 4·75 chocolate). The expected black thus appears, and the numbers are thus in close agreement with expectation. Cuénot (2), however, speaks of the appearance of blacks as unexpected. He attempts to account for them on his original scheme by representing black as the dense form of chocolate. This account is, however, inapplicable, for, as I shall show in detail, blue, not chocolate, is the dilute form of black, while chocolate has its own dilute form, silver fawn. This appears at once from the fact that both black × silver fawn and blue × chocolate alike give F_1 black, with 9 black, 3 blue, 3 chocolate, 1 silver fawn in F_2. Chocolate, therefore, equally with black, bears the factor for dense deposition.

The relation of the several colour determiners to each other is inadequately described by use of the terms dominant and recessive; and agouti, black, and chocolate must be regarded as composing a descending series in which black is epistatic* to chocolate, and agouti to both.

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* See Bateson, 'Science,' N.S., vol. 26, p. 653.

The term epistatic is thus applied to denote such a relationship between factors which are not in the same allelomorphic pair. A factor, then, is epistatic to another, when by its presence it conceals the existence of the other factor, although not allelomorphic to it. The terms dominant and recessive should only be applied to express relationship between factors in the same allelomorphic pair.

In dark-eyed mice, the inter-relations of all the colours are now clear, except in so far as yellow and its various combinations are concerned. My results agree with those of Cuénot and others in making it probable that yellows are always heterozygous, but various difficulties are encountered when a more precise statement is attempted. This part of the analysis must be deferred till more experimental data are obtained. The relation of yellow to the factor G is not yet clear. All that can yet be stated is that since G cannot be present in a black or chocolate,* not only the arrangement of the pigment in the agouti hairs, but also the presence of yellow pigment in them must be controlled by this factor.

EYE-COLOUR.

In addition to the factors for coat-colour, the determiners, on which eye-colour depends, have to be considered. It will be shown later that the development of certain coat-colours is also dependent upon these eye-colour determiners.

Mice can be grouped according to the colour of the eyes into two classes, dark-eyed and pink-eyed.

Dark-eyed Mice.—The eyes, viewed *in situ*, are apparently black. But when they are removed differences can be seen at once, and when sections of them are examined microscopically, these differences can be made out more fully. Apparently all mice, which have black pigment present in the coat, have black pigment in their eyes. Thus agouti and its various dilute forms, and black and blue, all have black eyes.

Those mice in which black pigment is absent from the coat, on the other hand, have only chocolate pigment in the eye. Thus, cinnamon agouti, and the dilute forms of cinnamon agouti, and chocolate and silver-fawn, all have chocolate eyes.

The fact that yellow mice have chocolate eyes has already been mentioned by Castle (3). In the clear yellows examined by me, the pigment was chocolate ; but, I find, that sooty yellow mice (*i.e.*, yellow mice with some black pigment present in the hairs, giving a sooty appearance) have black pigment in the eyes. Some of these mice appear to have only black pigment present in their eyes, but others have both black and chocolate pigments in their eyes. I do not know at present how these differences in eye-pigment in sooty yellow mice are related to differences in genetic behaviour.

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* Chocolate containing G is cinnamon agouti.

Ruby Eyes.—The so-called ruby eyes are dark with a red glow in them. They are not common, and three cases of them only have occurred in my breeding experiments. One was a piebald cinnamon agouti and white, one was a white mouse with one small patch of cinnamon agouti behind the right ear, and the third was a piebald chocolate and white. In each case, the iris was heavily pigmented with chocolate, and the choroid was only slightly pigmented with chocolate. No black pigment was found in either tissue.

Pink-eyed Mice are of many kinds.

(a) *The Albino.*—This type has apparently no dark colouring matter present, either in its eye or in its coat. I believe, however, that the whiteness of the coat is not due alone to the air in the spaces of the hair, but that a white substance of the nature of a pigment is present in the hairs (4).

(b) *Pink-eyed Mice with Coloured Coats.*—The eyes of these mice are only apparently unpigmented. Sections of them examined under the microscope show that both iris and choroid are pigmented, though very slightly.

The further description and the genetic behaviour of these mice will be dealt with later in another paper. Experiment has, however, already proved that their composition is very various. Several types of colour can be distinguished among the so-called pink-eyed "lilac" mice. They may, or may not, possess the factors B and D, and, consequently, when bred with chocolates, they may give blacks, blues, chocolates, or silver-fawns. So far as my experience goes, however, this mating never produces agouti.

DENSE AND DILUTE COLORATIONS.

The dense colour form is dominant over the dilute form. Thus black is dominant over blue, and chocolate is dominant over silver-fawn. Black is epistatic to chocolate, and it follows, therefore, that blue is epistatic to silver-fawn. All colours are dominant to albino. The offspring of a mating between a homozygous coloured mouse and an albino will be coloured, but the colour of the offspring will depend upon the epistatic determiner which may be carried by either parent.

Thus the offspring of a black mouse by an albino with chocolate determiner will be black, but the offspring of a chocolate mouse by an albino with black determiner will be black, because black is epistatic to chocolate.

Black.—Black when mated with albino with black determiner gives black in F_1. In the second generation F_2 there should be blacks and albinos in the ratio of 3 : 1.

The experimental numbers are—

Black.	Albino.
54	11

The calculated numbers are—

Black.	Albino.
48·75	16·25

Black when mated with chocolate gives black in F_1.

In F_2 there should be 3 blacks to 1 chocolate.

The experimental numbers are—

Black.	Chocolate.
42	17

The calculated numbers are—

Black.	Chocolate.
44·25	14·75

Black mated with albino carrying the chocolate determiner gives all black in F_1.

In F_2, according to calculation, there should be a ratio of—

9 black : 3 chocolate : 4 albino.

The experimental numbers are—

Black.	Chocolate.	Albino.
76	24	27

The calculated numbers are—

Black.	Chocolate.	Albino.
71·44	23·81	31·75

If these heterozygous blacks carrying both chocolate and albino are mated with albino with chocolate determiner, the results should follow a ratio of—

9 black : 3 chocolate : 12 albino.

The experimental numbers are—

Black.	Chocolate.	Albino.
18	5	27

The calculated numbers are—

Black.	Chocolate.	Albino.
18·75	6·25	25

Black is dominant over blue, because the concentrated colour is dominant over the weak.

Black × blue = black F_1.

In F_2 there should be a proportion of 3 blacks : 1 blue.

The experimental numbers are—

Black.	Blue.
50	13

The calculated numbers are—

Black.	Blue.
47·25	15·75

If the heterozygous black carrying blue be mated with an albino bearing dense and black determiners, the first generation will all be black. In the second generation there should result black, blue, and albino in the ratio of 9 : 3 : 4.

The experimental numbers are—

Black.	Blue.	Albino.
21	4	6

The calculated numbers are—

Black.	Blue.	Albino.
17·44	5·81	7·75

When black is mated with silver-fawn, the resulting offspring are black, because black is epistatic to chocolate, and the dense colour is dominant over the dilute. In dealing with the second generation, there are four factors to be taken into account—the two pigments, black and chocolate, and the concentration and dilution.

There should result in F_2, blacks, blues, chocolates, and silver-fawns, and the proportions should be in the ratio of—

9 black : 3 blue : 3 chocolate : 1 silver-fawn.

The experimental numbers are—

Black.	Blue.	Chocolate.	Silver-fawn.
67	21	20	5

The calculated numbers are—

Black.	Blue.	Chocolate.	Silver-fawn.
63·56	21·19	21·19	7·06

It is obvious, if the factors concerned in the mating be considered, that exactly the same result will be arrived at if a chocolate mouse be mated with a blue mouse. Here the chocolate mouse carries the factor of concentration, while the blue mouse is responsible for blackness.

From such matings, black mice must result in the first generation, since black is epistatic to chocolate and density is dominant over dilution. In the second generation there should be the same proportion, viz. :—

9 black : 3 blue : 3 chocolate : 1 silver-fawn.

The experimental numbers are—

Black.	Blue.	Chocolate.	Silver-fawn.
44	17	17	8

The calculated numbers are—

Black.	Blue.	Chocolate.	Silver-fawn.
48·375	16·125	16·125	5·375

The matings in which albinos are introduced as black × albino with silver-fawn determiner, or blue × albino with chocolate determiner, or silver-fawn × albino with black determiner, or chocolate × albino with blue determiner, should in the same way yield like results in F_2. There should be 27 blacks, 9 blue, 9 chocolate, and 3 silver-fawn, and 16 albino in the second generation. I have only worked out one of these matings fully. Blue was mated with albino with chocolate determiner.

The experimental numbers are—

Black.	Blue.	Chocolate.	Silver-fawn.	Albino.
33	10	8	2	12

The calculated numbers are—

Black.	Blue.	Chocolate.	Silver-fawn.	Albino.
27·42	9·14	9·14	3·05	16·25

Blue.—When blue is mated with silver-fawn, the resulting offspring are blue, and in the second generation there should be a proportion of 3 blue to 1 silver-fawn.

The experimental numbers are—

Blue.	Silver-fawn.
46	17

The calculated numbers are—

Blue.	Silver-fawn.
47·25	15·75

When the heterozygous blues from this mating are mated with silver-fawns there should be an equal number of blues and silver-fawns.

The experimental numbers are—

Blue.	Silver-fawn.
37	36

The calculated numbers are—

Blue.	Silver-fawn.
36·5	36·5

When blue is mated with albino with silver-fawn determiner the resulting offspring are blue.

In the second generation there should be a ratio of—

9 blue : 3 silver-fawn : 4 albino.

The experimental numbers are—

Blue.	Silver-fawn.	Albino.
55	26	36

The calculated numbers are—

Blue.	Silver-fawn.	Albino.
65·81	21·94	29·25

Chocolate.—Chocolate is dominant over silver-fawn. I have made this mating very often, always with the same result, chocolate offspring in F_1, but the matings were not carried into the second generation.

Chocolate mated with albino with chocolate determiner gives chocolate in the first generation.

In F_2 there should be 3 chocolate : 1 albino.

The experimental numbers are—

Chocolate.	Albino.
99	27

The calculated numbers are—

Chocolate.	Albino.
94·5	31·5

Heterozygous chocolate carrying albino mated with albino with chocolate determiner should give equal numbers of chocolate and albino.

The experimental numbers are—

Chocolate.	Albino.
14	15

The calculated numbers are—

Chocolate.	Albino.
14·5	14·5

Chocolate carrying albino mated with albino with silver-fawn determiner should give an equal number of albinos to coloured mice and a proportion of three chocolates to one silver-fawn.

The experimental numbers are—

Chocolate.	Silver-fawn.	Albino.
13	4	18

The calculated numbers are—

Chocolate.	Silver-fawn.	Albino.
12·75	4·25	18

Silver-fawn mated with albino carrying chocolate determiner gives all chocolate in F_1.

In F_2 there should be 9 chocolate : 3 silver-fawn : 4 albino.

The experimental numbers are—

Chocolate.	Silver-fawn.	Albino.
19	4	6

The calculated numbers are—

Chocolate.	Silver-fawn.	Albino.
16·31	5·44	7·25

Silver-fawn carrying albino mated with silver-fawn carrying albino should give 3 silver-fawn : 1 albino.

The experimental numbers are—

Silver-fawn.	Albino.
30	8

The calculated numbers are—

Silver-fawn.	Albino.
31·5	9·5

Piebald Mice.

Both Cuénot (2) and Allen (5) state that in mice the piebald condition behaves in accordance with Mendelian principles as a recessive character in relation to total pigmentation.

Cuénot also suggests that the forms which are only slightly piebald, that is, in which the patches of white are small and few, will dominate over those which, on the contrary, exhibit large and many patches of white; and also that when two of these latter are mated together their young will also be of the same character, bearing large and many patches of white.

In this connection the case of black-eyed whites may be given. These mice, which show no trace of colour in the fur, may be taken as representing the extreme case of piebald marking. I have not succeeded in obtaining a race of them which breeds true. The young are very various in appearance, ranging from black-eyed whites, through all grades of piebald marking to heavily pigmented forms, although, so far, no selfs have appeared.

In my experiments I have dealt with piebald mice of two kinds. One kind belongs to the class described already by Cuénot and Allen, and behaves as recessive to self-colour. That is, mated with self-coloured mice, these piebalds give only self-coloured young. In the second generation the piebald returns again in the proportion of one piebald to three selfs.

The experimental numbers are—

Self.	Piebald.
330	124

The calculated numbers are—

Self.	Piebald.
340·5	113·5

These piebalds mated with albinos with self determiner give only self-colours in the first generation. In the second generation there are selfs, piebalds, and albinos.

The experimental numbers are—

Self.	Piebald.	Albino.
259	90	125

The calculated numbers are—

Self.	Piebald.	Albino.
266·625	88·875	118·5

Albino mice can likewise carry piebald, viz., absence of the self-determiner. Mice of this kind mated with self-coloured mice homozygous as to self-character, give only selfs in the first generation. In the second generation selfs, piebalds, and albinos are obtained.

The experimental numbers are—

Self.	Piebald.	Albino.
163	53	69

The calculated numbers are—

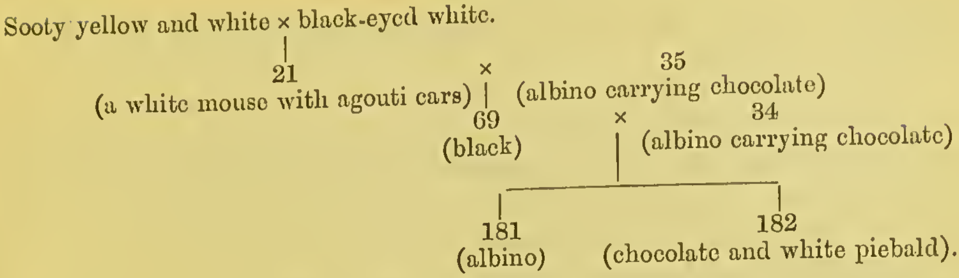
Self.	Piebald.	Albino.
160·31	53·44	71·25

Dominant Piebald.—But the second kind of piebald mouse behaves differently, and the piebald character, which it carries, behaves as a dominant. The mice of this class have all been derived from the union of a sooty yellow-and-white mouse, of unknown origin, with a black-eyed white mouse from Atlee, the well-known fancier. There is not enough evidence to show whether both, or if only one, which of the parents is responsible for the transmission of the dominant piebald character. Four of the descendants of these mice were mated with homozygous self mice, and threw 8 selfs and 13 piebalds. This suggests that they are DR in character, the piebald character being dominant. The piebalds of this class were inter-mated eight times, and gave 12 selfs and 44 piebalds.

The calculated numbers on the supposition of the mice being DR in character would be 14 selfs and 42 piebalds.

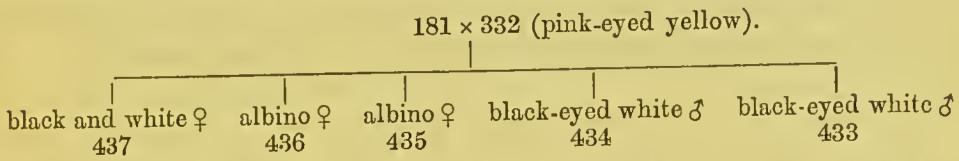
Intermatings between piebalds descended from the same union, which have been derived from matings with albinos, show likewise that the piebalds were able to produce self-coloured mice. From matings of this kind I have obtained 30 piebalds, 12 selfs, 27 albinos. The expected ratio is 9 : 3 : 4, which would give 38·25 piebalds, 12·75 selfs, 17 albinos, so the albinos are in distinct excess.

The inheritance of the black-eyed white character has been transmitted through these mice, and I will quote from the tables to show the descent in some detail.


Sooty yellow and white × black-eyed white.
21
(a white mouse with agouti ears)
×
35
(albino carrying chocolate)
69
(black)
×
34
(albino carrying chocolate)
181
(albino)
182
(chocolate and white piebald).

181 × 182 gave 4 albinos, 2 chocolate and white piebalds. These latter piebalds have given 10 chocolate and whites and 1 albino, but no selfs.

181, the albino, was mated with a pink-eyed, yellow mouse, which had been given to me by Mr. Darbishire. The resulting young were 2 black-eyed whites, 1 black and white piebald, and 4 albinos.



The piebald doe 437 was mated both with 434 and with 433, the black-eyed white bucks, and gave 4 piebalds, 2 selfs, and 8 albinos.

One of these albinos was mated with one of the piebalds, and gave 3 albinos and 3 piebalds. These latter piebalds gave 1 albino, 3 piebalds, and 1 self-coloured mouse.

435 (albino) was mated with a homozygous pink-eyed lilac mouse, and gave 2 piebald lilac and white pink-eyed mice, and from these lilac and white mice I obtained 4 piebalds, 2 selfs, and 4 albinos. 435 (albino) was also mated with a silver-fawn mouse, and gave 2 chocolate and white piebalds. From them I obtained 5 chocolate and white piebald, 2 silver-fawn and white piebald, 2 chocolate selfs, 1 silver-fawn self, 3 black-eyed whites, and 6 albinos.

A piebald from the union of 437 and 434, mated with a chocolate mouse, gave 3 chocolate and white piebalds, and from them I have obtained 15 chocolate and white piebalds, 4 chocolate selfs, and 4 black-eyed whites. From two of these black-eyed whites, I have obtained 4 black-eyed whites and 2 chocolate and white piebalds.

There are thus, genetically, two entirely distinct types of piebalds, which to the eye are indistinguishable. The genetic relations of these two types are as yet unknown.

Unconformable Case.

Finally, I must mention one case, which I am unable to account for. I bred a black doe, by mating a blue with a black. The parents were both homozygous. They never threw any albinos or chocolates in any of their litters. Nor did any of their offspring show any signs of being heterozygous.

The black doe, so obtained, was mated with five different albinos. She was taken from albino to albino. One of these albinos was descended from the dominant piebald race, and the result of this union was 3 albinos, 4 chocolates, and 1 chocolate and white piebald. Her other matings resulted in 21 blacks.

The albino was mated with two other homozygous blacks, and 6 blacks resulted; and mated with a homozygous chocolate, 6 chocolates resulted. Apart from the unconformable result, there was no reason to suspect any error in this case.

In conclusion, I offer my thanks to Mr. Bateson, for his kindness in giving both help and advice while I have been carrying on the experiments recorded.

The expenses of these experiments have been partly defrayed by grants from the Government Grant Fund of the Royal Society.

List of Mice.

Chocolate.—Only chocolate pigment present in the hair; the hairs are heavily loaded with pigment.

Silver-fawn.—Only chocolate pigment present, but in less amount than in the case of the chocolate mouse. This is the dilute form.

Black.—Both black and chocolate pigments are present; the hairs are heavily loaded with pigment.

Blue.—This is the dilute variety of the black.

Agouti.—This is also called golden agouti, and is the colour of the wild mouse. There are three pigments present in the hairs—yellow, black, and chocolate. The bases of the hairs are black, and the hairs are barred with yellow. Some hairs have no yellow in them and some are tipped with yellow.

There are several dilute forms of agouti known, according to whether all or only one of the pigments is diluted in amount.*

Cinnamon Agouti.—Both chocolate and yellow pigments are present, but no black, and the hairs are ticked as in the case of the agouti.

Dilute forms of the cinnamon agouti are also known.

Yellow.—The clear yellow appears to have only yellow pigment in its hairs. In the sooty yellow, black is always discoverable in the hairs with the aid of the microscope.

Cream is the dilute variety of yellow.

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* The terms golden agouti and cinnamon agouti are wrongly applied in the account given in "The Present State of Knowledge of Colour Heredity in Mice and Rats," W. Bateson, 'Zool. Soc. Proc.,' 1903, and should be as given above.

Sable.—All three pigments are found in the hairs of the sable mouse. The back is dark and ticked like agouti, but the flanks and belly are yellow.

Albino.—Apparently no coloured pigment in the coat or eyes.

The pink-eyed coloured mice will be described in another paper.

List of Authors.

(1) Bateson.—"Address to the Section of Cytology and Heredity. International Zoological Congress, 1907," 'Science,' N.S., vol. 26.
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ON SEX-INHERITANCE IN THE MOTH *ABRAXAS GROSSULARIATA* AND ITS VAR. *LACTICOLOR.*

By L. Doncaster, M.A., Lecturer on Zoology, Birmingham University.

(Communicated by W. Bateson, F.R.S.)

In the 'Proc. Zoo. Soc.,' 1906, vol. 1, p. 125 (with Plate VIII), a preliminary account was given by Doncaster and Raynor of the inheritance of the variety *lacticolor* of *Abraxas grossulariata.* This variety is a Mendelian recessive, differing from the type chiefly in the great reduction and somewhat different shape of the black markings. In the wild state it is exceedingly rare, and is found almost exclusively in the female.

Breeding experiments gave the following results:—

Lact. ♀ × *gross.* ♂ gave *gross.* ♂, *gross.* ♀.
Heterozygous *gross.* ♀ × heterozygous *gross.* ♂ gave *gross.* ♂, *gross.* ♀, *lact.* ♀.
Lact. ♀ × heterozygous *gross.* ♂ gave *gross.* ♂, *lact.* ♂, *gross.* ♀, *lact.* ♀.
Heterozygous *gross.* ♀ × *lact.* ♂ gave *gross.* ♂, *lact.* ♀.
Lact. ♀ × *lact.* ♂ gave *lact.* ♂, *lact.* ♀.

The important points about these results are: (1) that *lacticolor* males can be obtained by pairing a *lacticolor* female with a heterozygous male, in which case *lact.* ♂. *gross.* ♂, *lact.* ♀, *gross.* ♀, are obtained in roughly equal numbers (Table III below). (2) The converse cross, heterozygous female × *lacticolor* male gives all the males *gross.* (heterozygous), all the females *lact.* (Table IV).

In explanation of these facts it was suggested that the sex-determinants behave as Mendelian allelomorphs, segregating in gametogenesis, and that the *lacticolor* character was coupled with the female determinant. But it was assumed that both male and female individuals were heterozygous in respect of sex, and this resulted in making the whole hypothesis rather complicated.

A simpler explanation has been offered by Bateson and Punnett,* viz.: (1) that the sex-determinants behave as Mendelian allelomorphs, femaleness being dominant; (2) that female individuals are heterozygous in respect of sex, having the constitution ♀ ♂ and producing male-bearing and female-bearing eggs in equal numbers; males are homozygous, of constitution ♂ ♂ producing only male-bearing spermatozoa; (3) that there is repulsion between the determinant for femaleness and the *grossulariata* determinant in oogenesis, so that male-bearing eggs bear *grossulariata*, female-bearing eggs the *lacticolor* character.

We then get the following results from the various matings: ♂, ♀ representing the sex determinants; G, L the *gross.* and *lact.* characters respectively.

Parents.	Constitution.	Gametes.	Offspring.
Lact. female ………… *Gross.* ♂ ………………	LL♀♂ GG♂♂	L♀, L♂ G♂, G♂	LG♀♂ = *gross.* female LG♂♂ = *gross.* male
Heterozygous female … Heterozygous male ……	GL♀♂ GL♂♂	L♀, G♂ G♂, L♂	LG♀♂ = *gross.* female LL♀♂ = *lact.* female GL♂♂ = *gross.* male GG♂♂ = *gross.* male
Lact. female…………… Heterozygous male ……	LL♀♂ GL♂♂	L♀, L♂ G♂, L♂	LG♀♂ = *gross.* female LL♀♂ = *lact.* female LG♂♂ = *gross.* male LL♂♂ = *lact.* male
Heterozygous female … *Lact.* male ……………	GL♀♂ LL♂♂	L♀, G♂ L♂, L♂	LL♀♂ = *lact.* female GL♂♂ = *gross.* male

This explanation was thus in accordance with all the facts, and this year it has received important confirmation. For it now appears that when a wild *grossulariata* female is paired with a *lacticolor* male, all the male offspring are *grossulariata* and all the females *lacticolor*, *i.e.*, the same result is obtained with wild females which have never been crossed with the rare *lacticolor* variety, as is produced by pairing a first-cross *grossulariata* female with a *lacticolor* male.*

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* 'Science,' 1908, N.S., vol. 27, p. 785.

The wild females used in these experiments were derived from different parts of the country, some from districts in which *lacticolor* is unknown. It may, therefore, be regarded as certain that in the moth *Abraxas grossulariata* males are normally homozygous in respect of the *grossulariata* character, but all females are heterozygotes carrying recessive *lacticolor*. But since in oogenesis there is repulsion or incompatibility between the dominant *grossulariata* and the dominant female determinant, the male-bearing eggs all bear *grossulariata*, the female-bearing *lacticolor*.

Both kinds of eggs are fertilised by spermatozoa bearing determinants for maleness and the *grossulariata* character, and so homozygous males and heterozygous females are produced indefinitely. The exceptional and very rare production of a wild *lacticolor* must be due to some accidental disturbance of the association of the *grossulariata* determinant with the male-bearing egg.

The following tables give the detailed results of my experiments. Mr. Raynor's results subsequent to those already published are in agreement, with a small percentage of exceptions which are possibly due to accident. The exceptions are as follows: Among nine families, comprising 680 individuals, from the mating *gross.* ♀ × *lact.* ♂, three *grossulariata* ♀s were recorded, and one *lacticolor* ♂. Two *grossulariata* ♂s appeared in families from *lact.* ♀ × *lact.* ♂ (among 280 *lacticolor* individuals), and one *grossulariata* ♀ from wild ♀ × *lact.* ♂, among 54 *lacticolor* ♀s. Two *lacticolor* ♀s also appeared in a family from *lact.* ♀ × wild ♂.

Table I.—Lacticolor ♀ × grossulariata ♂ (wild).

Pairing.	Gross. ♂.	Gross. ♀.
'05.3	15	16
'07.3	30	34
Total	45	50

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* In some families of this type of mating there was a very large excess of females, and in one (No. 1907.19) no males were produced.

Table II.—Heterozygous ♀ × heterozygous ♂.

Pairing.	Gross. ♂.	Gross. ♀.	Lact. ♂.	Lact. ♀.
'04. 2	7	1	—	4
'07. 8	5	3	—	1
'07.13	2	—	—	2
Total	14	4	—	7

Table III.—Lacticolor ♀ × heterozygous ♂.

Pairing.	Gross. ♂.	Gross. ♀.	Lact. ♂.	Lact. ♀.
'06. 7	31	34	33	36
'06. 2	1	2	—	—
'06. 6	5	4	1	—
'07. 1	1	—	1	1
'07. 4	8	8	12	11
'07.15	—	2	3	2
'07.16	3	6	5	7
'07.22	4	—	1	2
'07.23	10	6	9	11
Total	63	62	65	70

Table IV.—Heterozygous ♀ × lacticolor ♂.

Pairing.	Gross. ♂.	Lact. ♀.
'06. 4	25	30
'06. 8	74	54
'06.18	13	10
'06.19	12	14
'06.21	17	16
'06.27	4	6
Total	145	130

Table V.—Wild ♀ × lacticolor ♂.

Pairing.	Gross. ♂.	Lact. ♀.
'07. 6	2	15
'07. 7	7	.7
'07.12	10	11
'07.19	—	19
Total	19	52

NOTE ON THE INHERITANCE OF SEX IN CANARIES.

By Florence M. Durham, Lecturer of Newnham College, Cambridge, and Dorothea C. E. Marryat.

(Communicated by W. Bateson, F.R.S. Received September 26, 1908.)

It has long been known to fanciers of canaries that certain curious results occur when cinnamons are mated with other varieties. The cinnamon canary is so called on account of the colour of its plumage, which is of a brownish tint, due to the presence of a chocolate melanin and the absence of black melanin. The green canary has both pigments present in its feathers. The most definite feature of the cinnamon is, however, the colour of the eye in the newly-hatched bird. In ordinary canaries the eyes on hatching look black, but in cinnamons they look pink. The eyes become dark in appearance as the bird grows older, so that in the adult cinnamon it is extremely difficult, if not quite impossible, to distinguish the colour of its eye from that of a common canary by simple inspection. Microscopical examination, however, shows that the pigment of the cinnamon eye is different from that of the normal eye, being chocolate only, and not black. All birds with black in their feathers have black in their eyes.

All birds with cinnamon feathers are, of course, cinnamons, and have had pink eyes on hatching; but it should be premised that birds may be in plumage pure yellow, owing to the absence of melanins, and it is not possible by examination of a yellow bird during life to tell whether it was originally pink-eyed or black-eyed.

To avoid ambiguity, the cinnamons will be referred to as pink-eyed and the other varieties as black-eyed.

The pink-eyed character is a Mendelian recessive, and the offspring of two pink-eyed birds is always pink-eyed.

When pink-eyed and black-eyed varieties are bred together, the fanciers are agreed that the results are as follows :—

1. Pink-eyed hen and black-eyed cock gives all young of both sexes black-eyed.

2. Black-eyed hen and pink-eyed cock will give all *male* offspring black-eyed. The female offspring are most commonly pink-eyed; black-eyed hens may occur, but all the *pink-eyed offspring are hens* without exception, so far as is known.

Statements to this effect are made in most of the books on canary breeding. A particularly full account is given by Mr. C. L. W. Noorduijn,* who has also been good enough to answer several questions on this subject.

We commenced our experiments three years ago, for the purpose of investigating the problem constituted by this peculiar inheritance. These experiments are still in progress, but as the phenomena are so closely parallel to those discovered by Doncaster in the case of *Abraxas grossulariata* and its variety *lacticolor*, it seems desirable to publish a preliminary account of the work at the present time.

The results obtained have been as follows :—

Mating.	Offspring.			
	♀.		♂.	
	B.	P.	B.	P.
1. P♀ × B♂	7		19	
2. B♀ × P♂	4	33	30	
3. B♀ × F_1 B♂ ...	18	13	24	
4. F_1 B♀ × F_1 B♂ ...	1	2	2	
5. P♀ × F_1 B♂ ...	24	21	5	19
6. F_1 B♀ × P♂		6	4	

B, black-eyed. P, pink-eyed.

On comparing these results with Doncaster's for *Abraxas grossulariata*, it is evident that there is a close agreement between the two sets of phenomena, except in so far that whereas the mating No. 2, dominant ♀ × recessive ♂, has in the canaries sometimes given dominant ♀s, these were not proved to occur in the corresponding families of *grossulariata*. With this exception, therefore, the interpretation suggested for that case by Bateson and Punnett† can be applied to the results in the canaries. The female is taken as being heterozygous in sex, femaleness being a dominant, and the male is regarded as homozygous in the absence of femaleness. The black-eyed character B is a dominant and the pink-eyed character b (absence of B) is recessive.

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* 'Album der Natuur,' 1903, p. 71.

† 'Science,' vol. 27, N.S., 1908, p. 785.

In the ordinary case in which black-eyed ♀ × pink-eyed ♂ gives black-eyed cocks and pink-eyed hens, the assumption that there is spurious allelomorphism or repulsion between femaleness and B gives a consistent representation of the facts. The ordinary black-eyed hen is thus ♀ ♂Bb, and her ova are respectively ♀b and ♂B. The black-eyed cock is ♂ ♂BB. The pink-eyed cock is ♂ ♂bb, and the pink-eyed hen is ♀ ♂bb. The matings 1, 2, 3, and 5 of the previous table can thus be represented as follows:—

1.		Pink-eyed ♀	×	black-eyed ♂.
	Composition......	bb ♀ ♂		BB ♂ ♂
	F_1	black-eyed hens ♀ ♂ Bb		black-eyed cocks ♂ ♂ Bb
2.		Black-eyed ♀	×	pink-eyed ♂.
	Composition......	Bb ♀ ♂		bb ♂ ♂
	Gametes	B ♂ b ♀		all b ♂
	F_1	pink-eyed hens bb ♀ ♂		black-eyed cocks Bb ♂ ♂
3.		Black-eyed ♀	×	black-eyed F_1 ♂.
	Composition......	Bb ♀ ♂		Bb ♂ ♂
	Gametes	B ♂ b ♀		B ♂ b ♂
	Result	black-eyed hens Bb ♀ ♂ pink-eyed hens bb ♀ ♂		black-eyed cocks BB ♂ ♂ and also Bb ♂ ♂
5.		Pink-eyed ♀	×	black-eyed F_1 ♂.
	Composition......	bb ♀ ♂		Bb ♂ ♂
	Result	black-eyed hens Bb ♀ ♂ pink-eyed hens bb ♀ ♂		black-eyed cocks Bb ♂ ♂ pink-eyed cocks bb ♂ ♂

Matings 4 and 6 in the previous table need not be represented here, because they are in reality identical with No. 3 and No. 2 respectively, for the black-eyed hens, whether they come from a pink-eyed mother or not, are, in fact, heterozygous in the black-eye and pink-eye characters.

Whatever be the truth regarding the transmission of sex, there is thus no escape from the remarkable conclusion that just as the normal females of the moth *Abraxas grossulariata* are in reality hybrids in the *lacticolor* character, so the ordinary black-eyed hen canaries are hybrids in the pink-eye character.

Though the general course of the phenomena can be thus represented, two difficulties remain. The first is that mentioned above, that black-eyed hens have been produced by the mating black-eyed hen × pink-eyed cock. Only two of our hens have behaved in this way, and unfortunately we know nothing of the origin of these birds. No suggestion can be offered yet as to the causation of these departures from the usual rule.

Lastly, though but for the exceptional results, the scheme suggested successfully represents the qualitative features of the inheritance, the quantitative results are not according to expectation. It may be observed, however, that the departures affect the relative numbers of the two sexes as much as those of the varieties, and of course the scheme presupposes numerical equality between the output of males and females in each case. Curiously enough in the first series of the *Grossulariata* experiments, similarly wide departures from this equality were observed,* though in the later series the numbers showed fair simplicity and steadiness. We have as yet no clue to the meaning of these larger fluctuations, which are repeatedly encountered, when the output of the sexes is observed under experimental conditions.

We have to thank Professor Bateson for his help and advice. The expenses are in part defrayed by a grant from the Government Grant Fund.

CORRIGENDA TO REPORT III.

Page 20. In pedigree at top, for ♂ 253 read ♂ 144.
" 20. Delete note at bottom of page.
" 23. In Exp. 200, for "r.s. × r.r." read "s. × r.r."
" 29. In Exp. 378 the figure 31 should come under the column headed p. instead of under that headed s.

By an unfortunate mistake it is stated in Report III that *two separate factors* are concerned in producing hoariness besides those which produce colour. The error arose through a misinterpretation made in earlier stages of the analysis, which was carelessly retained after each of the results on which it was based had been otherwise elucidated. The diagrams of tables there given are correct otherwise, and show clearly that *one* hoariness-factor is required in addition to the two colour-factors.

We are indebted to Mr. Doncaster for this important correction.

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* Doncaster and Raynor, 'P.Z.S.,' 1906, vol. 1, pp. 130—131.

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REPORTS TO THE EVOLUTION COMMITTEE OF THE ROYAL SOCIETY.

REPORT V.

EXPERIMENTAL STUDIES IN THE PHYSIOLOGY OF HEREDITY.

By M. Wheldale, D. C. E. Marryat, and I. B. J. Sollas.

FURTHER OBSERVATIONS UPON THE INHERITANCE OF FLOWER-COLOUR IN *ANTIRRHINUM MAJUS.*

By M. Wheldale.

(Received July 6, 1909.)

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Preliminary Statement of Results.

In a previous paper* it has been shown, as a result of cross-breeding, that flower-colour in *Antirrhinum majus* may be represented by several Mendelian factors. Further matings have been made with types not hitherto used, chiefly with a view to finding out the significance of the various shades of magenta and the manner of inheritance of striping in the corolla. About thirteen thousand plants have been recorded since the publication of the first paper, and the results obtained have necessitated some extension of the original solution, though, at the same time, they have amply verified this solution as previously stated; in all, some sixteen thousand plants have been grown, and, except for the remarkable anomaly in regard to the behaviour of the striped forms (see p. 7), the whole mass of results can now be expressed in terms of Mendelian factors.

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* 'Roy. Soc. Proc.,' B, vol. 79, 1907. See also E. Baur, 'Beihefte z. Med. Klin.,' 1908, who has made independently many confirmatory experiments with *A. majus*, showing also that the several colour-types can be produced in the peloric forms.

In addition, extracts have been made of the pigments from most varieties, and the behaviour of such pigments towards certain chemical reagents has been investigated.

The final results may be stated as follows :—

1. The original wild *Antirrhinum majus* has *magenta* flowers, the colour being due to a pigment of the anthocyanin class. The production of this pigment depends on the presence in the plant of certain organic substances, accompanied probably by certain ferments (all representable by Mendelian factors). Numerous horticultural varieties have arisen from time to time through loss from the type of the power to produce either the ferments or the organic bodies upon which the ferments act.

2. Broadly speaking, the magenta anthocyanic pigment may be regarded as an oxidation product of a chromogen, in nature allied to the flavone series of colouring matters;* the oxidation is brought about probably through the agency of an oxydase.

3. The loss of power to produce the oxydase (representable by a Mendelian factor) from the zygote gives rise to a variety bearing *ivory-white* flowers. This variety is incapable of forming anthocyanin, but contains a pale yellow chromogen, which will be termed the ivory chromogen.

4. A variety bearing *yellow* flowers arises from the ivory-white by loss of a further constituent, possibly a ferment (again representable by a Mendelian factor). The yellow colour is due to the presence in the superficial cells of the lips of the corolla of a so-called xantheïc (soluble yellow) pigment, also of a flavone nature, and which will be termed the yellow chromogen. The yellow chromogen appears to be modified by the ferment with the production of the ivory chromogen. Hence, plants from which the power to form either the oxydase or the modifying ferment is absent are incapable of producing anthocyanin and bear flowers, having the lips of the corolla yellow, though the tube is ivory-white.

5. The yellow chromogen can also be acted upon by the oxydase, the result being the production of a *crimson* anthocyanin. Thus the variety containing both the oxydase and the yellow chromogen bears crimson flowers.

6. Complete absence of any chromogen, both of the ivory and the

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* Wheldale, "On the Nature of Anthocyanin," 'Cam. Phil. Soc. Proc.,' vol. 15, part 2, 1909.

yellow, from the zygote results in a true albino bearing *pure white* flowers, and incapable of producing any pigment. The albino, however, can carry either the oxydase or the modifying ferment or both.

7. Ivory, then, may be said to be epistatic to yellow; magenta and crimson epistatic to ivory and yellow respectively.

8. The oxidation of the chromogen by the oxydase appears to be a complex process, in that it takes place in two stages, and is in itself due to two factors; one factor produces a tingeing only of magenta, whereas a second, concentration factor, intensifies this to the full magenta of the wild type. The concentration factor cannot show unless the tingeing factor is also present.

9. The production of magenta colour in the corolla tube must be represented by a factor which is inherited independently of the lip factor. There is between them, however, a relation such that magenta colour only shows in the tube if the same colour is also present in the lips. On the other hand, the oxydase may be absent from the tube but present in the lips; this condition gives rise to the "*delila*" varieties, in which the lips are magenta or crimson of various shades, while the tube is ivory-white.

10. Formation of the yellow chromogen has not been found to occur in the tube (except locally, *see* 11); hence the tube is never yellow, and in crimson varieties the tube is magenta, of an intensity corresponding to the intensity of the crimson in the lips.

11. In the type, and in all varieties except the albino, there is local production of the yellow chromogen in a patch on the palate and in two rows of hairs on the inner surface of the tube. These areas are not, as a rule, invaded by the red pigment.

12. Sometimes the concentration factor (mentioned in 8) occurs locally in streaks and gives rise to striped forms. Striping behaves as a Mendelian allelomorph to the concentration factor in the unstriped condition, and is recessive to it. To the tingeing factor, striping is dominant, zygotes *homozygous* in the striping factor show magenta stripings on an *ivory* ground. Those *heterozygous* in the striping factor show magenta stripings on a *tinged* ground; hence the latter are heterozygous forms and never breed true. Every striped magenta has its delila form, and, in addition, its counterpart in the crimson series. In other words, we find the curious result that the operation of the factors which cause tingeing to be developed in the tube is altered by the presence of the concentration factor in its striped state. This influence is such that when the plant is homozygous for this factor all the tingeing disappears from the spaces between the stripes, though if the plant were heterozygous for the factor which causes the concentration-stripes the interspaces would be tinged.

The nature and behaviour of striped forms have not yet been adequately investigated. I have, however, met with the definite anomaly recorded by de Vries, that striped forms throw some self-coloured offspring in proportions not as yet determined.

DETAILS OF PIGMENTATION, VARIETIES, AND FACTORS.

Magenta colour in *Antirrhinum* is due to anthocyanin in the cells of the corolla. There are at least four distinct shades of magenta, depending on different degrees of concentration of the anthocyanin, and borne on zygotes of different constitution. It has been found useful to describe these varieties as :—

Tinged Ivory,* tingeing of anthocyanin in the corolla.
Pale Magenta.
Intermediate Magenta, similar to the wild *Antirrhinum* colour.
Deep Magenta.

Alcoholic extracts from flowers of these varieties give solutions, in proportionate depth, of a red colour inclined to purple. The pigment is also soluble in water, and is precipitated by copper and lead acetates as green precipitates of definite shades for each shade of magenta. No concentration nor dilution of the extract appears to alter the shade of green; hence we may conclude that each shade of magenta is due to the presence of some definite organic compound.†

The various shades of magenta are due to different combinations of factors in the zygote, as will be shown later.

When the power of producing the oxydase is absent from the zygote, the flowers are ivory-white,‡ and the variety is known as *ivory*. To the eye no colour is apparent in the corolla (apart from the palate and hairs); an alcoholic extract is pale yellow, and gives a bright canary-yellow colour, with strong acids and alkalis, a precipitate of the same shade with basic lead acetate, and a brown-black colour with iron salts. Such reactions indicate the presence of a flavone colouring matter.

Through the loss of some body, possibly a ferment as suggested above, the flavone of the ivory-white variety gives rise to a more highly coloured lemon-yellow pigment, of the xantheïc class, in the superficial cells of the lips, and gives the variety known as *yellow*. The pigment is identical with that found locally in the palate and tube of the previous varieties. It is soluble in water to a deep yellow solution, which is turned orange-red by strong acids and alkalis, and is precipitated by copper and lead acetates as bright-red precipitates.

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* Termed "rose" in the previous paper, 'Roy. Soc. Proc.,' B, vol. 79.

† Details as to the reactions of anthocyanin are given in 'Cam. Phil. Soc. Proc.,' *loc. cit.* See also this Report, p. 26.

‡ Except for the local patches of yellow pigment on the palate and in hairs on the interior of the tube.

Total loss of chromogen from the zygote gives an *albino* variety. The alcoholic extract in this case contains no pigment, and does not give the characteristic canary-yellow colour with acids and alkalis nor the precipitate with lead salts. Albinism here may be regarded as loss of both red and yellow pigments.

When anthocyanin is formed from the xantheïc pigment acting as chromogen, the resulting colour is crimson. Every shade of magenta has its corresponding shade of crimson, so that we find the varieties :—

Tinged Yellow corresponding with *Tinged Ivory.*
Pale Crimson corresponding with *Pale Magenta.*
Intermediate Crimson corresponding with *Intermediate Magenta.*
Deep Crimson corresponding with *Deep Magenta.*

The evidence for regarding anthocyanin as the oxidation product of a chromogen has been given elsewhere.*

In *Antirrhinum*, the magenta and crimson pigments are precipitated by lead acetate as bright and dull green precipitates respectively; the green colour being due to admixture of the yellow or orange-red (from the ivory or yellow chromogen), with the blue given by the oxidised product, anthocyanin, in the presence of alkali.

Further, from results of breeding, it has been shown that anthocyanin is not manifested in the zygote unless the factors representing either the yellow or the ivory chromogen are present. In other words, anthocyanin can only exist on an ivory or a yellow ground, not on an albino.

Of late years, another variety of *Antirrhinum* has appeared, known commercially as "Rose Doré." The pigment is carmine pink in colour, and exists in various degrees of concentration. It is evidently a derivative of the magenta pigment, but as to how or when it exactly appeared there seems to be no evidence. Like the magenta, it can only exist on an ivory or yellow ground, producing in the latter case a brilliant orange—"Orange King."

The "Rose Doré" pigment is soluble in water, giving a similarly coloured solution, and it is precipitated by lead acetate as a red precipitate; hence it is not turned blue by alkalis. The pigment is of interest, in that, combined in a zygote with intermediate magenta sap colour, it deepens the latter shade of magenta or crimson to *deep magenta* or *deep crimson* varieties.

It appears, then, that the character, flower-colour, in *Antirrhinum* must be represented by at least six Mendelian factors, the presence, absence, and combinations of which give rise to the numerous horticultural varieties.

Though certain relationships exist between the factors, they are not allelomorphic to each other, but to their absence in each case. They may be represented as follows :—

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* 'Cam. Phil. Soc. Proc.,' *loc. cit.*

Y. A factor representing a yellow chromogen of the nature of a flavone (xantheïc pigment), in the lips; with this is correlated the presence of an ivory chromogen, also of the nature of a flavone, in the tube, and a local occurrence of the above yellow chromogen in two rows of hairs on the inner surface of the tube.

I. A factor representing a ferment possibly, which acts upon the yellow chromogen—Y—to form a less highly coloured ivory chromogen in the lips (except for a patch of yellow chromogen remaining on the palate). I cannot be manifested except in the presence of Y.

L. A factor representing an oxydase producing magenta tingeing in the lips when acting upon the ivory chromogen (palate still yellow). When acting upon the yellow chromogen in the absence of I the tingeing is crimson.

T. A factor representing the presence of the oxydase producing magenta tingeing in the tube. T cannot be manifested unless L is also present. Since the formation of the yellow chromogen never occurs in the tube (except locally in hairs), the latter is never crimson.

D. A factor representing some body, again probably a ferment, which causes concentration or deepening of the magenta tingeing, and produces the anthocyanin of the wild type. It is manifested only when Y or I together with L and T are also present.

The carmine pink of "Rose Doré" is also representable by a factor, which depends for its manifestation on the presence of the yellow or ivory chromogen. In the presence of intermediate magenta or crimson it gives a still deeper type, deep magenta or crimson.

The factors having been given, it will now be shown how they may be combined to produce the various forms.

A zygote of the constitution—YYIILLTTDD has *intermediate magenta* flowers—probably the wild *Antirrhinum* colour.

The colour remains unaltered when the zygote is heterozygous in Y, I, T, or D; but if the zygote is heterozygous in L, *i.e.* of the constitution—YYIILlTTDD—the flowers are *pale magenta*. Except among the striped forms, to be considered later, pale magenta is the only heterozygous form found and can, of course, never be fixed.

Loss of D, the concentration factor, gives a zygote—YYIIllTTdd—with *tinged ivory* flowers. D cannot be manifested unless L is also present.

Loss of T, presence of oxydase in the tube, gives a variety known as "delila," in which the tube is ivory-white, while the lips may either be tinged or of a pale or intermediate magenta colour.

YYIILLttDD is *Intermediate magenta delila.*
YYIILlttDD ,, *Pale magenta delila.*
YYIILLttdd ,, *Tinged ivory delila.*

T cannot be manifested unless L be also present in the zygote, that is, there can be no magenta colour in the tube unless there is also magenta pigment in the lips. There is, moreover, a correlation between lip and tube colour such that the tube always takes the same concentration as the lips.

Loss of L, presence of oxydase in the lips, gives *ivory*—YYIIllTTDD. Since T and D cannot show unless L is present, an ivory may bear T or D, both or neither, *i.e.* YYIIllTTdd, YYIIllttDD, or YYIIllttdd.

Loss of I, the modifying ferment, gives *yellow*, when L is also absent —YYiillTTDD. Yellow, like ivory, may carry T or D, both or neither. The addition of L, T, and D gives a series of forms containing the oxidised yellow chromogen, the resulting colour being some shade of crimson of which a series exists corresponding to the shades of magenta:—

YYiiLLTTdd is *T. yellow.*
YYiiLLttdd ,, *T. yellow delila.*
YYiiLlTTDD ,, *P. crimson.*
YYiiLlttDD ,, *P. crimson delila.*
YYiiLLTTDD ,, *I. crimson.*
YYiiLLttDD ,, *I. crimson delila.*

Loss of Y gives *white*—yyIILLTTDD. The albino may be homo- or hetero-zygous in any of the other factors, since they are none of them manifested except in the presence of Y. Even apart from the absence of yellow colour on the palate the albino is quite distinguishable from the ivory.

Striped Forms.

In certain striped forms of *Antirrhinum* the body represented by the concentration factor D does not occur in all cells of the corolla, but is localised in streaks and irregular blotches (in which case S may be substituted for D). When the zygote is heterozygous in L the streaks, as would be expected, are pale magenta, when homozygous in L the streaks are intermediate magenta in colour.

It has been shown that in non-striped forms flower-colour is the same whether the zygote is homo- or hetero-zygous in D. But striped forms, heterozygous in S, have magenta stripings on a ground tinged with magenta, whereas, when they are homozygous in S, the ground colour between the stripings is ivory.

The four zygotic types may be represented as follows:—

1. YYIILLTTSS …… *Ivory striped with I. magenta.*
2. YYIILlTTSS …… *Ivory striped with P. magenta.*
3. YYIILLTTSs …… *T. ivory striped with I. magenta.*
4. YYIILlTTSs …… *T. ivory striped with P. magenta.*

Corresponding delila and crimson varieties occur with the loss of T and I respectively; 3 and 4 are heterozygous forms which never breed true but always throw 1 and 2. The T ivory—to the ivory-striped always occur in the proportion 2 : 1, as also the pale to the intermediate magenta striped.

When striped forms are crossed with tinged forms the striping is, as would be expected, dominant.

When striped forms are crossed with whole magenta forms the concentration factor in the form of striping is allelomorphic and recessive to the normal condition, so that striped × non-striped gives non-striped crossbreds.

Though striping, on the whole, behaves as a Mendelian character, yet the theoretical and experimental results may not always agree very closely, since a striped individual is liable at any time to produce non-striped individuals. A small percentage of non-striped are usually found among the offspring of a striped form.* These sports do not, however, materially affect the validity of the inheritance.

The "White Queen" Series.

A variety was mentioned in the previous paper (p. 289), which appeared to be a white with yellow pigment on the palate and in hairs on the tube. This variety is known commercially as "*White Queen.*" Apart from the yellow patch on the palate it is indistinguishable, even to the experienced eye, from the true albino. When mated with albinos and yellows it revealed itself to be an ivory, and in F_2 a yellow was extracted rather paler in colour than the yellow used in all other matings. This paler yellow, of which "White Queen" is the ivory type, gives when L, T, and D are added, a series perfectly comparable to the series from the deeper yellow, but differing in that all the varieties of the former are a shade paler, due undoubtedly to the paler fundamental yellow.

Mated together, the paler is dominant to the deeper yellow. It is possible that "White Queen," especially as it is slighter and smaller in habit than majus, may be derived from another species of *Antirrhinum.*

DETAILS OF MATINGS.

The constitution of all varieties used in the following matings is based upon the Mendelian system already stated. The validity of this

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* De Vries, 'Species and Varieties,' 1905, p. 315.

(*To face p. 9.*)

Table I.—F_1 from Matings of certain Ivories and Yellows × Whites.

	W 1 yy Ii Ll Tt DD	W 2 yy Ii Ll Tt DD	W 3 yy II LL TT DD	W 5 yy Ii Ll Tt DD	W 6 yy Ii ll – – DD	W 7 yy II Ll Tt DD	W 8 yy – – Ll TT DD	W 9 yy Ii ll – – DD	W 10 yy Ii Ll – – DD	W 14 yy II Ll TT DD	W 15 yy Ii LL Tt DD	W 16 yy Ii LL Tt DD	W 17 yy Ii LL Tt DD	W 18 yy II LL Tt DD	W 19 yy Ii Ll TT DD	W 20 yy II LL TT DD	W 22 yy Ii Ll Tt DD
I 2 Yy Ii ll tt DD	Magenta Magenta delila Crimson Crimson delila Ivory Yellow White	Magenta Magenta delila Crimson Crimson delila Ivory Yellow White	Magenta White								Magenta Magenta delila Crimson Crimson delila White				Magenta Crimson Ivory Yellow White	Magenta White	Magenta Magenta delila Crimson Crimson delila Ivory Yellow White
I 3 Yy II li tt DD	Magenta Magenta delila Ivory White	Magenta Magenta delila Ivory White	Magenta White	Magenta Magenta delila Ivory White	Ivory White	Magenta Magenta delila Ivory White	Magenta Ivory White	Ivory White			Magenta Magenta delila White	Magenta Magenta delila White		Magenta Magenta delila White	Magenta Ivory White	Magenta White	Magenta Magenta delila Ivory White
Y 1 Yy ii ll TT DD	Magenta Crimson Ivory Yellow White													Magenta White	Magenta Crimson Ivory Yellow White	Magenta White	Magenta Crimson Ivory Yellow White
Y 2 YY ii ll –t DD	Magenta Magenta delila Crimson Crimson delila Ivory Yellow	Magenta Magenta delila Crimson Crimson delila Ivory Yellow	Magenta	Magenta Magenta delila Crimson Crimson delila Ivory Yellow		Magenta Magenta delila Ivory	Magenta	Ivory Yellow			Magenta Magenta delila Crimson Crimson delila	Magenta Magenta delila Crimson Crimson delila	Magenta Magenta delila Crimson Crimson delila	Magenta Magenta delila	Magenta Crimson Ivory Yellow		Magenta Magenta delila Crimson Crimson delila Ivory Yellow
Y 4 YY ii ll TT DD									Magenta Crimson Ivory Yellow	Magenta Ivory						Magenta	
Y 5 YY ii ll TT DD									Magenta Crimson Ivory Yellow	Magenta Ivory							
Y 6 Yy ii ll tt DD										Magenta Ivory White							

W 1—22 are whites, I 2—3 ivories and Y 1—6 yellows, of known parentage. The zygotic composition of each is given. – denotes that the presence or absence of any factor cannot be deduced from known data.

solution can be tested by a comparison of the theoretical and experimental results in all cases.

A. *Further Details of Matings recorded in Previous Paper.*

1. *White × Yellow, striped with Pale Crimson.*—In the light of further results as regards the factors producing magenta colour, the parents may be represented as :—

yyIILLttDD …… White
YYiiLlTtDD …… Yellow striped P. crimson[*]

and both may be assumed to be homozygous in D, since T. ivory does not appear in F$_2$. If Diagram I be consulted in the previous paper, and if the additional factor I be added, there will be found to be 27 kinds of whites in F$_2$. To prove the validity of this statement, matings were made between ivories and yellows of known constitution and a number of F$_2$ and F$_3$ whites extracted from the above cross.

The results are set out in the accompanying Table I.[†]

From this table it is seen that 3 ivory and 7 yellow individuals were in all crossed with 23 whites. The constitution of each white has, when possible, been deduced from the F$_1$ results; in no case is there any contradiction in the results obtained by crossing two or more individuals with the same type.

To some extent, the constitution of the whites can be predicted from their parentage: whites 1—14 and 18—22, for instance, being extracted from Case (i),[‡] may be homo- or hetero-zygous in I, L, and T. Whites 15, 16, and 17 must be homozygous in L, since they are extracted from Case (ii). White 30 is an F individual extracted from a yellow in Case (iii); hence it can only be carrying D.

Ivory 3, from evidence supplied by its offspring, was found to be homozygous in I, so that the F from it × any white can never throw yellow or crimsons.

Yellows 4 and 5 are extracted from crimsons, and hence must be homozygous in T; the F$_1$, from their matings with whites can therefore never show delilas, and so forth.

All crimsons and magentas in this series are pale, since they must be heterozygous in L, ivory and yellow being unable to carry these factors.

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[*] This individual behaves as non-striped—an exception which may occur in striped strains; normally striping would reappear in F$_2$.

[†] To reduce the size of Table I, the following additional combinations, which have also been made, are omitted from it:—I 1 (YyIIllttDD) × W23 (yyiilltttDD) gave ivory and white. I 3 × W 4 (yy – – LlTtDD), magenta, magenta delila, ivory and white. Y 3 (YYiill – – DD) × W 6, ivory and yellow. Y 4 × W 11 (yyiiLl – – DD), crimson and yellow; × W 12 (yyIIll – – DD), ivory; × W 13 (yyIill – – DD), ivory and yellow. Y 6 × W 21 (yyiill – – DD), yellow and white. Y 7 (YYiill-tDD) × W 15, × W 16 and × W 17, gave in each case magenta, magenta delila, crimson and crimson delila.

[‡] 'Roy. Soc. Proc.,' *loc. cit.*, p. 293.

In connection with these matings, it is worth while to record that W 23 was also crossed with I. crimson and I. crimson delila.

The parents may be represented as :—

yyiilltt DD, White × YYiiLLTTDD ... I. crimson .... Case (i).
YYiiLLttDD ... I. crimson delila... Case (ii).

The crossbreds :—

Case (i). YyiiLlTtDD ...... P. crimson (P. crimson 36).*
Case (ii). YyiiLlttDD ...... P. crimson delila (P. crimson delila 41).

F_2, from Case (i), consisted of P. and I. crimson, P. and I. crimson delila, yellow and white.

F_2, from Case (ii), consisted of P. and I. crimson delila, yellow, and white. The numbers in both cases are too small to be worth recording.

2. *White* × *Yellow.*—

Parents :—

yyIILLttDD ...... White.
YYiillttDD .... Yellow.

Crossbreds :—

YyIiLlttDD, P. magenta delila ...... (P. magenta delila 21).

F_2 consisted of P. and I. magenta delila, P. and I. crimson delila, ivory, yellow, and white. Numbers too small for record.

3. *Yellow* × *Intermediate Crimson.*
× *Intermediate Crimson Delila.*

Parents :—

YYiillttDD, Yellow × YYiiLLTTDD ... I. crimson .... Case (i).
× YYiiLLttDD ... I. crimson delila ... Case (ii).

Crossbreds :—

Case (i). YYiiLlTtDD ... P. crimson (P. crimson 23).
Case (ii). YYiiLlttDD ... P. crimson delila (P. crimson delila 22).

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* Varieties and numbers in brackets here signify those obtained experimentally.

F_2 :—

Varieties in F_2.	Ratios.		Numbers calculated.	Numbers observed.
Case (i).—P. crimson × self, from 3 plants.				
Crimson (P. and I.)	9	YLTD ...	41 ·1	51
Crimson (P. and I.) delila ...	3	YLD	13 ·6	11
Yellow............................	3	YTD	18 ·2	11
Yellow............................	1	YD	—	—
Total	16	—	72 ·9	73
Case (ii).—P. crimson delila × self, from 2 plants.				
Crimson (P. and I.) delila ...	3	YLD	88 ·5	89
Yellow............................	1	YD	29 ·5	29
Total	4	—	118 ·0	118

B. *Tinged Ivory* × *other Varieties.*

1. *Tinged Ivory* × *Yellow striped Pale Crimson.*—

Parents :—

YYIILLTTdd ...... T. ivory.
YYiiLlTtDD .... Yellow striped P. crimson.*

Crossbreds :—

Case (i).	YYIiLlTtDd ...	P. magenta	(P. magenta 8).
Case (ii).	YYIiLlTTDd ...	P. magenta	
Case (iii).	YYIiLLTtDd ...	I. magenta	(I. magenta 9).
Case (iv).	YYIiLLTTDd ...	I. magenta	

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* The same individual used in cross with white, see p. 9.

F_2 :—

Varieties in F_2.	Case (i).—P. magenta × self, from 3 plants.				Case (ii).—P. magenta × self, from 7 plants.				Case (iii).—I. magenta × self, from 5 plants.				Case (iv).—I. magenta × self, from 1 plant.			
	Ratios.		Numbers calculated.	Numbers observed.	Ratios.		Numbers calculated.	Numbers observed.	Ratios.		Numbers calculated.	Numbers observed.	Ratios.		Numbers calculated.	Numbers observed.
Magenta (P. and I.)	81	YILTD	58·5	67	27	YILTD	255·6	275	27	YILTD	105·0	113	9	YILTD	55·7	54
Magenta (P. and I.) delila	27	YILD	19·5	18	...	...	...	...	9	YILD	35·0	37				
T. ivory	27	YILT	19·5	17	9	YILT	85·2	67	9	YILT	35·0	28	3	YILT	18·6	16
Ivory..........................	27	YITD	34·7	41	9	YITD	113·6	121								
Crimson (P. and I.)	27	YLTD	19·5	21	9	YLTD	85·2	80	9	YLTD	35·0	34	3	YLTD	18·6	22
T. ivory delila	9	YIL	6·5	10	...	...	...	...	3	YIL	11·7	18				
Ivory..........................	9	YID	—	—												
Ivory..........................	9	YIT	—	—	3	YIT	—	—								
T. yellow	9	YLT	6·5	2	3	YLT	28·3	26	3	YLT	11·7	12	1	YLT	5·6	7
Crimson (P. and I.) delila	9	YLD	6·5	...	...	...	...	...	3	YLD	11·7	5				
Yellow	9	YTD	11·6	8	3	YTD	37·8	37								
Ivory..........................	3	YI	—	—												
T. yellow delila	3	YL	2·2	1	...	...	...	...	1	YL	3·9	2				
Yellow	3	YD	—	—												
Yellow	3	YT	—	—	1	YT	—	—								
Yellow	1	Y	—	—												
Totals..............	256	...	185·0	185	64	...	605·7	606	64	...	249·0	249	16	...	98·5	99

The P. and I. magentas will always be grouped together for simplification in F_2.

The F_3 generation has been obtained from Cases (ii) and (iv) only. If a diagram, similar to Diagram I in the previous paper, is constructed for F_2 from Case (ii), it will be found that the proportion of magentas heterozygous in L, *i.e.* pale magentas to those homozygous in L., *i.e.* intermediate magentas, is as 2 : 1. The experimental numbers have been found to agree in this respect. From the same diagram it is evident, from the offspring they will give in F_3, that there are 8 kinds of magenta, 4 of crimson, 4 of tinged ivory, 2 of tinged yellow, 2 of ivory, and 1 of yellow. All these have been found experimentally, as shown in the table on p. 14.

As regards Case (iv), the magentas, tested by their offspring in F_3, are of 4 kinds, the crimsons of 2, tinged ivories of 2, tinged yellows of 1. Such of these, as were found experimentally, are given in the following table:—

Number of F_2 plants selfed.	Colours of F_2 plants.	Constitution of F_2 plants.	Colours in F_3.			
			I. magenta.	I. crimson.	T. ivory.	T. yellow.
	I. magenta...	YYIILLTTDD	× *			
	,, ...	YYIILLTTDd	×	...	×	
2	,, ...	YYIiLLTTDD	60 (58)	18 (20)		
1	,, ...	YYIiLLTTDd	34 (33)	10 (11)	13 (11)	1 (3)
2	I. crimson ...	YYiiLLTTDD	...	55 (55)		
2	,, ...	YYiiLLTTDd	...	51 (51)	...	17 (17)
	T. ivory	YYIILLTTdd	...	...	×	
1	,, ...	YYIiLLTTdd	...	...	54 (51)	14 (17)
1	T. yellow ...	YYiiLLTTdd	...	...	...	60 (60)

* × denotes that the variety was not found experimentally.

2. *Tinged Ivory* × *Intermediate Crimson.*—

Parents :—

YYIILLTTdd ...... T. ivory.
YYiiLLTtDD ...... I. crimson.

Crossbreds :—

Case (i). YYIiLLTtDd ...... I. magenta
Case (ii). YYIiLLTTDd ...... I. magenta } (I. magenta 25).

Cases (i) and (ii) are identical with Cases (iii) and (iv) in previous cross; hence details of constitution need not be given.

Number of F_2 plants selfed.	Colour of F_2 plants.	Constitution of F_2 plants.	Colours in F_3.							
			Pale magenta.	Inter-mediate magenta.	Pale crimson.	Inter-mediate crimson.	Tinged ivory.	Tinged yellow.	Ivory.	Yellow.
3	I. magenta...	YYIILLTTDD	...	127 (127)*						
7	,, ...	YYIiLLTTDD	...	210 (209)	...	69 (70)				
5	,, ...	YYIILLTTDd	...	132 (137)	...	...	51 (46)			
6	,, ...	YYIiLLTTDd ...	...	106 (106)	...	37 (36)	34 (36)	13 (12)		
3	P. magenta	YYIILlTTDD ...	34 (34)	18 (17)	...	...	...	...	16 (17)	
6	,,	YYIILlTTDd ...	113 (103)	43 (52)	...	...	45 (52)	...	75 (69)	
9	,,	YYIiLlTTDD ...	183 (153)	52 (77)	57 (51)	19 (26)	...	...	75 (77)	24 (26)
8	,,	YYIiLlTTDd ...	120 (107)	50 (53)	34 (35)	19 (18)	54 (53)	7 (18)	71 (71)	24 (24)
3	I. crimson ...	YYiiLLTTDD...	...	...	...	92 (92)				
2	,, ...	YYiiLLTTDd ...	...	...	...	47 (44)	...	12 (15)		
1	P. crimson...	YYiiLlTTDD ...	...	...	4 (5)	1 (3)	...	...	...	5 (2)
4	,, ...	YYiiLlTTDd ...	...	...	35 (42)	20 (21)	...	24 (21)	...	31 (27)
3	T. ivory	YYIiLlTTdd ...	...	...	...	...	55 (60)	24 (20)	22 (20)	6 (7)
8	,, ...	YYIiLLTTdd ...	...	...	...	...	225 (231)	83 (77)		
3	,, ...	YYIILlTTdd ...	...	...	...	...	102 (98)	...	29 (33)	
6	,, ...	YYIILLTTdd...	...	...	...	...	247 (247)			
1	T. yellow ...	YYiiLlTTdd ...	...	...	...	...	...	27 (26)	...	8 (9)
2	,, ...	YYiiLLTTdd ...	...	...	...	...	...	64 (64)		
5	Ivory.........	YYIIllTTDD (Dd or dd)	...	...	...	...	...	...	154 (154)	
5	,, ...	YYIillTTDD (Dd or dd)	...	...	...	...	...	...	84 (87)	32 (29)
9	Yellow	YYiillTTDD (Dd or dd)	...	...	...	...	...	...	...	312 (312)

F_2 :—

Varieties in F_2.	Case (i).—I. magenta × self, from 7 plants.		Case (ii).—I. magenta × self, from 6 plants.	
	Numbers calculated.	Numbers observed.	Numbers calculated.	Numbers observed.
I. magenta	159·0	167	182·2	180
I. magenta delila.........	53·0	50		
I. crimson..................	53·0	53	60·7	67
I. crimson delila	17·7	13		
T. ivory......................	53·0	58	60·7	63
T. ivory delila	17·7	13		
T. yellow	17·7	15	20·2	14
T. yellow delila	5·9	8		
Totals	377·0	377	323·8	324

3. *Tinged Ivory* × *Intermediate Crimson Delila.*—

Parents :—

YYIILLTTdd .... T. ivory.
YYiiLLttDD........... I. crimson delila.

Crossbreds :—

YYIiLLTtDd .... I. magenta (I. magenta 30).

These are identical with Case (i) in the previous cross.

F_2 :—

Varieties in F_2.	I. magenta × self, from 17 plants.	
	Numbers calculated.	Numbers observed.
I. magenta	360·7	399
I. magenta delila	120·2	122
I. crimson	120·2	121
I. crimson delila	40·1	38
T. ivory	120·2	88
T. ivory delila	40·1	35
T. yellow............................	40·1	33
T. yellow delila	13·3	19
Totals	854·9	855

The following table shows qualitatively the results in F_3. Too few plants were grown to make the numbers worth recording.

Colours of F_2 plants.	Constitution of F_2 plants.	Colours in F_3.							
		I. magenta.	I. magenta delila.	I. crimson.	I. crimson delila.	T. ivory.	T. ivory delila.	T. yellow.	T. yellow delila.
I. magenta	YYIILLTTDD	×							
,,	YYIILLTTDd								
,,	YYIILLTtDd								
,,	YYIiLLTTDD	×	...	×					
,,	YYIILLTtDD								
,,	YYIiLLTtDD								
,,	YYIiLLTTDd	×	...	×	...	×	...	×	
,,	YYIiLLTtDd	×	×	×	×	×	×	×	×
T. ivory	YYIiLLTtdd	...	...	...	...	×	×	×	×

4. *Tinged Ivory* × *Ivory.*—

× *Tinged Yellow Delila.*
× *Yellow.*

For sake of convenience, these matings may be grouped together.

Parents :—

YYIILLTTdd ... T. ivory × YYIIllTtdd ... Ivory .... Case (i).
× YYiiLLttdd ... T. yellow delila ... ,, (ii).
× YYiilltt DD ... Yellow .... ,, (iii).

Crossbreds :—

Case (i). { YYIILlTTdd ...... T. ivory } (T. ivory 20).
{ YYIILlTtdd ...... ,, }
Case (ii). YYIiLLTtdd ...... ,, (T. ivory 36).
Case (iii). YYIiLlTtDd ...... P. magenta (P. magenta 150).

(See Table on p. 18.)

C. " *White Queen* " × *Other Varieties.*

The " White Queen " individual used in crossing was breeding true, since it gave on selfing 107 offspring like itself; it can be represented as YYIIllttDD.

1. " *White Queen* " × *White.*
× *Yellow.*

F_1 :—

Varieties in F_1.	Varieties crossed with " White Queen."			
	White I. yyIiLLTTDD.	White II. yyiiLLTtDD.	White III. yyiillttDD.	Yellow. yyiillttDD.
P. magenta	81 (81)	157 (161)		
P. magenta delila ...	...	165 (161)		
Ivory	...	...	69 (69)	209 (209)

Varieties in F_2.	Case (i).						Case (ii).			Case (iii).		
	Ratios.	Numbers calculated.	Numbers observed.	Ratios.	Numbers calculated.	Numbers observed.	Ratios.	Numbers calculated.	Numbers observed.	Ratios.	Numbers calculated.	Numbers observed.
Magenta (P. and I.)	...	...	...	...	...	...	...	...	...	81	...	22
Magenta (P. and I.) delila	...	...	...	...	...	...	...	...	...	27	...	9
Crimson (P. and I.)	...	...	...	...	...	...	...	...	...	27	...	10
Crimson (P. and I.) delila	...	...	...	...	...	...	...	...	...	9	...	8
T. ivory	3	54·8	59	9	14·1	16	9	98·4	104	27	...	6
T. ivory delila	...	...	...	3	4·7	4	3	32·8	32	9	...	1
T. yellow	...	...	...	...	...	...	3	32·8	31	9	...	2
T. yellow delila	...	...	...	...	...	...	1	10·9	8	3	...	1
Ivory	1	18·2	14	4	6·2	5	...	...	...	48	...	21
Yellow	...	...	...	...	...	...	...	...	...	16	...	4
Totals	4	73·0	73	16	25·0	25	16	174·9	175	256	—	84

All varieties were obtained in Case (iii), though the numbers are too small to be of value.

F_2 was obtained from the cross with white I. :—

Varieties in F_2.	Ratios.		Numbers calculated.	Numbers observed.
		P. magenta × self from 3 plants.		
Magenta (P and I) ………………	81	YILTD …	52 ·8	84
Magenta (P and I) delila ……	27	YILD …	17 ·7	18
Crimson (P and I) ……………	27	YLTD …	17 ·7	12
Crimson (P and I) delila ……	9	YLD ……	5 ·9	1
Ivory ………………………………	27	YITD……	23 ·7	22
Ivory ………………………………	9	YID ……	—	—
Yellow …………………………	9	YT ………	7 ·9	6
Yellow …………………………	3	YD ………	—	—
White …………………………	64	—— ……	41 ·9	25
Totals ………………	256	…	167 ·6	168
		P. magenta × self from 3 plants.		
Magenta (P and I) ………………	27	YILTD …	71 ·2	80
Magenta (P and I) delila ……	9	YILD …	23 ·7	33
Ivory ………………………………	9	YITD …	31 ·6	29
Ivory ………………………………	3	YID ……	—	—
White …………………………	16	—— ……	42 ·2	27
Totals ………………	64	…	168 ·7	169

D. *Striped Forms × other Varieties.*

Striped Forms × Tinged Ivory.

1. *Tinged Ivory × Tinged Ivory striped Pale Magenta.*—

Parents :—

YYIILlTtSs …… T. ivory striped P. magenta.
YYIILLTTss …… T. ivory.

Crossbreds :—

Case (i).	YYIILlTtSs ……	T. ivory striped P. magenta.	(T. ivory striped magenta 10.)
„ (ii).	YYIILlTTSs ……	T. ivory striped P. magenta.	
„ (iii).	YYIILLTTSs ……	T. ivory striped I. magenta.	
„ (iv).	YYIILLTtSs ……	T. ivory striped I. magenta.	
„ (v).	YYIILLTTss ……	Tinged ivory	(T. ivory 15.)
„ (vi).	YYIILLTtss ……	„ „	
„ (vii).	YYIILlTTss ……	„ „	
„ (viii).	YYIILlTtss ……	„ „	

F_2: only Cases (i), (ii), and (viii) were obtained experimentally:—

Varieties in F_2.	Case (i). T. ivory striped P. magenta × self from 3 plants.				Case (ii). T. ivory striped P. magenta × self from 1 plant.				Case (viii). T. ivory × self from 2 plants.			
	Ratios.		Numbers calculated.	Numbers observed.	Ratios.		Numbers calculated.	Numbers observed.	Ratios.		Numbers calculated.	Numbers observed.
T. ivory striped magenta (P. and I.)...	27	YILTS ...	103·3	92	9	YILTS ...	11·2	10				
Ivory striped magenta (P. and I.) ...												
T. ivory striped magenta (P. and I.) delila	9	YILS......	34·4	32								
Ivory striped magenta (P. and I) delila												
T. ivory....................................	9	YILT ...	34·4	33	3	YILT ...	3·7	7	9	YILT ...	24·2	19
Ivory....................................	9	YITS......	61·2	69	3	YITS......	5·0	3				
T. ivory delila	3	YIL	11·5	19	...	...	...	...	3	YIL	8·1	6
Ivory	3	YIT	—	—	1	YIT	—	—	3	YIT	10·7	18
Ivory	3	YIS	—	—								
Ivory	1	YI	—	—	...	...	...	...	1	YI	—	—
Totals	64	...	244·8	245	16	...	19·9	20	16	...	43·0	43

If a diagram be constructed for F_2 from Case (i) it will be seen that there are eight kinds of striped forms; four can be detected by appearance and the remainder by the offspring they give in F_3. The following table shows how far the experimental and theoretical results agree :—

Number of F_2 plants selfed.	Colour of F_2 plants.	Constitution of F_2 plants.	T. ivory striped P. magenta.		T. ivory striped I. magenta.		Ivory striped P. magenta.		Ivory striped I. magenta.		T. ivory.		Ivory.
			Whole.	Delila.	Whole.	Delila.	Whole.	Delila.	Whole.	Delila.	Whole.	Delila.	
1	Ivory striped I. magenta	YYIILLTTSS	...	...	...	...	...	...	24 (24)				
1	,, ,,	YYIILLTtSS	...	...	...	...	...	...	25 (24)	7 (8)			
	Ivory striped P. magenta	YYIILlTTSS ...	...	...	...	...	—	...	—	...	...	...	—
2	,, ,,	YYIILlTtSS ...	...	...	...	...	24 (24)	7 (8)	11 (11)	4 (4)	...	...	16 (15)
4	T. ivory striped I. magenta	YYIILLTTSs	...	...	104 (112)	...	...	...	58 (56)	...	62 (56)		
	,, ,,	YYIILLTtSs ...	...	...	—	—	...	...	—	—	—	—	
2	T. ivory striped P. magenta	YYIILlTTSs ...	27 (26)	...	9 (13)	...	11 (13)	...	10 (7)	...	27 (20)	...	21 (26)
4	,, ,,	YYIILlTtSs ...	52 (60)	17 (30)	45 (30)	9 (15)	22 (30)	*	11 (15)	†	58 (45)	13 (15)	95 (80)
1	Ivory striped I. magenta delila	YYIILLttSS ...	...	...	...	...	...	...	...	43 (43)			
2	Ivory striped P. magenta delila	YYIILlttSS ...	...	...	...	...	...	38 (43)	...	24 (21)	...	...	27 (25)
	T. ivory striped I. magenta delila	YYIILLttSs ...	...	—	...	...	...	...	...	—	...	—	
2	T. ivory striped P. magenta delila	YYIILlttSs ...	...	17 (20)	...	12 (10)	...	*	...	†	...	13 (10)	11 (13)
1	T. ivory	YYIILLTTss ...	...	...	...	...	...	...	...	...	11 (11)		
1	,,	YYIILlTTss ...	...	...	...	...	...	...	...	...	8 (8)	...	2 (2)
1	,,	YYIILLTtss ...	...	...	...	...	...	...	...	...	21 (26)	13 (8)	
3	,,	YYIILlTtss ...	...	...	...	...	...	...	...	...	56 (52)	14 (17)	22 (23)
2	T. ivory delila	YYIILLttss ...	...	...	...	...	...	...	...	...	...	24 (24)	
2	,, ,,	YYIILlttss ...	...	...	...	...	...	...	...	...	...	28 (28)	9 (9)
6	Ivory	YYIIllTTss ... Tt or tt	...	...	...	...	...	...	...	...	...	...	159 (159)

* Included in T. ivory striped P. magenta delila, from which it is not readily distinguishable.
† Included in T. ivory striped I. magenta delila.

2. *Tinged Ivory × Ivory striped Intermediate Magenta Delila.*—

Parents :—

YYIILLttSS …… Ivory striped I. magenta delila.
YYIILLTTss …… T. ivory.

Crossbreds :—

YYIILLTtSs …… T. ivory striped I. magenta (T. ivory striped I. magenta 63).

F_2 : not yet obtained.

3. *Tinged Ivory × Yellow striped Intermediate Crimson.*—

Parents :—

YYIILLTTss …… T. ivory.
YYiiLLTtSS …… Yellow striped I. crimson.

Crossbreds :—

Case (i). YYIiLLTtSs … T. ivory striped I. magenta.
Case (ii). YYIiLLTTSs … T. ivory striped I. magenta.
(T. ivory striped I. magenta 102.)

Varieties in F_2.	Ratios.		Numbers calculated.	Numbers observed.
		Case (i).—T. ivory striped I. magenta × self from 3 plants.		
T. ivory striped I. magenta ……… Ivory striped I. magenta……………	27	YILTS …	69 ·2	60
T. ivory striped I. magenta delila … Ivory striped I. magenta delila ……	9	YILS ……	23 ·0	21
T. yellow striped I. crimson ……… Yellow striped I. crimson …………	9	YLTS …	23 ·0	30
T. yellow striped I. crimson delila Yellow striped I. crimson delila …	3	YLS …	7 ·7	9
T. ivory………………………………	9	YILT …	23 ·0	22
T. ivory delila ………………………	3	YIL ……	7 ·7	8
T. yellow ……………………………	3	YLT ……	7 ·7	12
T. yellow delila ……………………	1	YL………	2 ·6	2
Totals …………………	64	…	163 ·9	164

Varieties in F_2.	Ratios.		Numbers calculated.	Numbers observed.
	Case (ii).—T. ivory striped I. magenta × self from 7 plants.			
T. ivory striped I. magenta .... Ivory striped I. magenta..............	9	YILTS ...	160·8	159
T. yellow striped I. crimson .... Yellow striped I. crimson	3	YLTS ...	53·6	49
T. ivory	3	YILT......	53·6	53
T. yellow	1	YLT	17·8	25
Totals	16	...	285·8	286

Striped Forms selfed.

Tinged Ivory striped Intermediate Magenta × *Self.*—

Evidence was obtained from the offspring of this individual, selfing being carried out to F_3.

Parent plant:—

YYIiLLTtSs.

F_1:—

Ratios.	Constitution of F_1 plants.	Colours of F_1 plants.	Numbers observed.
27	YILTS	T. ivory striped I. magenta*	28
9	YILS	T. ivory striped I. magenta delila	9
9	YILT............	T. ivory	7
9	YLTS............	T. yellow striped I. crimson....................	9
3	YLS	T. yellow striped I. crimson delila	1
3	YIL	T. ivory delila	3
3	YLT	T. yellow..	2
1	YL	T. yellow delila	1
64	...	Totals	60

* Includes individuals homozygous in S, *i.e.* ivory-striped magenta, since these were difficult to distinguish owing to the distribution of the striping in this particular case.

From a diagram for F_1, the constitution of the different varieties will be evident; the table below shows which of these varieties were found experimentally:—

Number of F_1 plants selfed.	Colour of F_1 plants.	Constitution of F_1 plants,	Colours in F_2.											
			T. ivory striped I. magenta.		Ivory striped I. magenta.		T. yellow striped I. crimson.		Yellow striped I. crimson.		T. ivory.		T. yellow.	
			Whole.	Delila.	Whole.	Delila.	Whole.	Delila.	Whole.	Delila.	Whole.	Delila.	Whole.	Delila.
1	T. ivory striped I. magenta	YYIILLTTSs...	9 (11)	...	Not distinguishable from previous form		...	...	Not distinguishable from previous form,		6 (4)			
2	,, ,, ...	YYIILLTtSs ...	35 (33)	14 (11)	...	...	...	...	...	. .	7 (11)	3 (4)		
2	,, ,, ...	YYIiLLTTSs...	45 (51)	...	...	...	13 (17)	...	...	...	22 (17)	...	9 (4)	
	,, ,, ...	YYIiLLTtSs ...	—	—	—	—	—	—	—	—	—	—	—	—
1	Ivory striped I. magenta............	YYIILLTTSS	...	...	22 (22)									
1	,, ,, ...	YYIILLTtSS...	...	...	3 (3)	1 (1)								
1	,, ,, ...	YYIiLLTTSS	...	...	57 (59)	...	22 (20)							
2	,, ,, ...	YYIiLLTtSS ...	...	...	30 (26)	8 (9)	5 (9)	3 (2)						
	Tinged ivory striped I. magenta delila	YYIILLttSs ...	...	—	...	...	...	...	...	...	...	—		
1	,, ,, ,,	YYIiLLttSs ...	...	23 (19)	...	...	...	4 (6)	...	...	...	4 (6)	...	2 (2)
1	Ivory striped I. magenta delila...	YYIILLttSS ...	...	36 (36)										
1	,, ,, ,,	YYIiLLttSS ...	...	15 (17)	...	...	...	...	7 (5)					
2	Yellow striped I. crimson	YYiiLLTtSS ...	...	...	...	...	...	...	74 (74)	25 (25)				
2	Yellow striped I. crimson delila	YYiiLLttSS ...	...	...	...	...	...	...	...	34 (34)				
3	T. ivory	YYIiLLTTss ...	...	...	...	...	...	...	...	...	77 (74)	...	21 (24)	
1	T. yellow	YYiiLLTTss ...	...	...	...	...	...	...	...	...	...	...	31 (31)	

Striped Forms × *Whole Forms.*—The intensifying factor D, when uniformly distributed over the corolla, is dominant to S, the condition when it is localised in stripes, that is, D and S are allelomorphic and unstriped flowers are dominant to striped. This is shown in the following crosses:—

Case (i).

Yellow striped I. crimson × white gave in F_1 164 P. crimson.
(YYiiLLTTSS.) (yyiillttDD.) (YyiiLlTtDS.)

Case (ii).

Yellow striped I. crimson delila × white gave in F_1 8 P. crimson delila.
(YYiiLLttSS.) (yyiillttDD.) (YyiiLlttDS.)

Case (iii).

Ivory striped I. magenta delila × I. magenta gave in F_1 181 I. magenta.
(YYIILLttSS.) (YYIILLTTDD.) (YYIILLTtDS.)

Case (iv).

Ivory striped I. magenta delila × yellow gave in F_1 110 P. magenta.
(YYIILLttSS.) (YYiillTTDD.) (YYIiLlTtDS.)

The F_2 from Cases (i) and (ii) was as follows:—

Colours in F_2.	Ratios.		Numbers calculated.	Numbers observed.
Case i.—P. crimson × self from 5 plants.				
P. crimson	81	YLTD ...	81	100
I. crimson				
P. crimson delila	27	YLD	27	24
I. crimson delila				
Yellow	27	YTD	48	60
Yellow striped P. crimson	27	YLT	27	25
Yellow striped I. crimson				
Yellow striped P. crimson delila ...	9	YL	9	5
Yellow striped I. crimson delila ...				
Yellow	9	YT	—	...
Yellow	9	YD	—	...
Yellow	3	Y	—	...
White	64	——	64	42
Totals	256	...	256	256

Colours in F_2.	Ratios.		Numbers calculated.	Numbers observed.
Case ii.—P. crimson delila × self from 1 plant.				
P. crimson	27	YLD	21·9	29
I. crimson				
Yellow striped P. crimson	9	YL	7·3	5
Yellow striped I. crimson				
Yellow	9	YD	9·7	8
Yellow	3	Y	—	—
White	16	—	13·0	10
Totals	64	...	51·9	52

In conclusion, I should like to express my thanks to Professor Bateson for his advice and help in connection with these experiments.

NOTE ON THE PHYSIOLOGICAL INTERPRETATION OF THE MENDELIAN FACTORS FOR COLOUR IN PLANTS.

By Miss M. Wheldale, Fellow of Newnham College, Cambridge.

(Communicated by W. Bateson, F.R.S. Received August 21, 1909.)

The genetic relations of numerous colour-varieties of Stocks and Sweet Peas are known, but so far no successful attempt has been made to discover the differences in chemical composition which these colour-differences must denote. The following experiments show reasons for regarding these varieties as terms in a series of oxidation-processes.

It is now a well-established fact that crosses between certain strains of white-flowered Sweet Peas and Stocks give purple-flowered offspring in which the colour is due to anthocyanin.* Similarly, among the F_2 extracted whites from such a cross, some individuals mated together give coloured offspring, others white only. Therefore, though indistinguishable to the eye, some F_2 whites must be physiologically different from others, and it has always been hoped that chemical tests might be devised which would distinguish between the various F_2 whites.

The Sweet Peas and Stocks used in the experiments to be described were kindly provided by Prof. Bateson and Miss Saunders, to whom I am much indebted not only for material to work upon, but also for advice and information in connection with the genetics of flower-colour.

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* Bateson, Saunders, and Punnett, 'Rep. Evol. Com. Roy. Soc.,' III.

1. *Test for Oxydases.*

It has been previously suggested* that the various red and blue plant pigments (anthocyanin) are oxidised products of substances of the nature of flavones, the agents of oxidation being oxydases. In Stocks and Sweet Peas all non-anthocyanic varieties, *i.e.* white and cream, have been found to contain a colourless flavone (chromogen), and in accordance with the above suggestion the coloured varieties contain the chromogen in certain stages of oxidation. Hence the loss of power to produce colour in these whites and creams is not due to *absence of chromogen*, and some other cause for albinism must be sought. The alternative of connecting lack of colour with loss of an oxidising ferment led to the idea of testing the flowers for oxydases.

On the basis of the theory of Chodat and Bach,† an oxydase may be represented as a system peroxide-peroxydase. The system as a whole is capable of blueing guaiacum tincture (direct action), whereas the peroxydase alone requires the addition of hydrogen peroxide to produce blue colour (indirect action).

In view of this conception, extracts of both coloured and white flowers of known gametic constitution were tested with guaiacum and hydrogen peroxide, and the resulting action was found to vary in different cases.

Of the coloured (anthocyanic) Stocks tested three classes can be distinguished:—

(1) True reds, *e.g.*, terra-cotta and a more dilute form, flesh-colour.
(2) Bluish reds, *e.g.*, one or more shades of crimson and the more dilute forms, rose and lilac.
(3) Purple, *e.g.*, deep purple and one or more pale shades.

Of Sweet Peas, two classes only :—

(1) Reds, *e.g.*, Tinged White (Red Picotee), Painted Lady, and Miss Hunt.
(2) Purples, *e.g.*, Purple Picotee, Purple Invincible (viz., bicolor with blue wings), and Purple bicolor with purple wings.

That the flowers in the above classes contain distinct substances, *i.e.* definite oxidation stages of the chromogen, is indicated by the different and constant colour reactions given by each class with certain chemical reagents, such as alkalis, iron salts, basic lead acetate, ammonium molybdate, etc.

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* Wheldale, M., 'Roy. Soc. Proc.,' B, vol. 81, 1909; 'Cam. Phil. Soc. Proc.,' vol. 15, Part 2, 1909.

† "Recherches sur les Ferments Oxydants," 'Arch. d. Sciences Phys. et Nat.,' 1904, Geneva.

The method employed in testing for oxydases is as follows:—The flowers are ground with powdered glass and absolute alcohol, and allowed to stand for about 24 hours; the alcohol is then filtered off, and the residue after drying is extracted with water. To the extract guaiacum tincture is added, either alone or together with hydrogen peroxide.

The following results were obtained:—

1. All coloured varieties of Stocks and Sweet Peas gave some direct and a strong indirect action.

2. Extracted F_2 white Sweet Peas from the cross round-pollened × long-pollened Emily Henderson* gave direct and indirect actions in certain degrees of intensity. The round-pollened parent gave a stronger direct action than the long-pollened parent.

3. Extracted F_2 white Stocks from the cross white glabrous × cream glabrous† also gave direct and indirect actions in varying degrees of intensity. The white glabrous parent gave a stronger direct action than the cream glabrous parent.

4. Among the whites from a rose Stock throwing rose, flesh and white, individuals were found which gave a strong indirect action while others gave a weak, the proportion of strong to weak being approximately 3 : 1.

5. Whites from a crimson Stock throwing crimsons and whites only all behaved alike.

The above results can be interpreted on the assumption that the following bodies are involved in the formation of flower-colour:—(1) Some organic substance (X) capable of functioning as a peroxide. (2) A peroxydase acting upon the peroxide with the production of active (atomic) oxygen. (3) A second ferment or activator reoxidising the peroxide‡ from molecular oxygen supplied by the air or from other sources. (4) A chromogen (C) capable of oxidation by means of active oxygen set free by the peroxydase. (5) The oxidised chromogen or anthocyanin.

On this supposition, albinism might result from the loss of power to produce either the peroxydase or the activator ferment,§ since the mechanism for transferring oxygen from the air to the chromogen would, under these circumstances, be incomplete. There should thus be two forms of albino, one due to loss of activator, the other to loss of peroxydase; two such albinos mated together should produce colour, for in the offspring the mechanism for colour-production is again complete.

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* 'Rep. Evol. Com.,' III, p. 31.

† 'Rep. Evol. Com.,' III, p. 38.

‡ Chodat suggests that the peroxide may sometimes be of a ferment nature—"un corps complexe participant de la nature des ferments." "Les Ferments Oxydants," 'Jour. Suisse de Chimie et Pharmacie,' 1905.

§ This is a more reasonable suggestion than loss of peroxide, which is possibly, like the chromogen, a body of metabolic significance. In the case of *Antirrhinum*, albinos exist from which the chromogen is absent, in addition to those containing chromogen only; the former are always less vigorous vegetatively than the latter. Since all whites in Sweet Peas and Stocks are equally vigorous, loss of ferment rather than peroxide seems the more probable cause of albinism.

We may, then, conveniently represent the factors for colour as A_1 activator and P_1 peroxydase, the two, in combination with a peroxide X_1, forming an oxydase system capable of acting on the chromogen (flavone) with the production of *red* anthocyanin.

Bluish-red and purple forms of anthocyanin may be represented as due to the action of an additional blueing oxydase *upon the product of the action of* A_1P_1, though the former is unable to act directly upon the unaltered chromogen. The blueing oxydase may be expressed as A_2 activator, P_2 peroxydase, and X_2 peroxide.

Taking into consideration the behaviour of oxydases in general, A_1 will, in all probability, only activate X_1 and A_2 in the same way X_2, but it is quite conceivable that P_1 may act with A_2X_2 and P_2 with A_1X_1 to produce the bluish-red forms of anthocyanin. Thus one variety of crimson would result from the presence in the plant of the system $A_1X_1P_1 + A_1X_1P_2$, another from the system $A_1X_1P_1 + A_2X_2P_1$, whereas purple is the product of the system $A_1X_1P_1 + A_2X_2P_2$.

2. *Test for a Reducing Factor.*

The existence in Stocks of dilute varieties, such as flesh, rose, etc., is dependent upon an additional factor I, of a limiting (reducing) nature, which prevents the whole action from taking place. Extracts from these varieties have a greater reducing action upon soluble Prussian blue solution than those from deeply coloured varieties. This action of the reducing factor is lessened or destroyed by treating the petals with absolute alcohol.

Similarly in Sweet Peas, the wings of the type Purple Invincible and the variety Painted Lady contain such a limiting factor, loss of which gives rise to the varieties purple-winged Purple Invincible and Miss Hunt; the latter have more deeply coloured wings in which more oxidation has taken place.

It follows, therefore, that the dominance in Stocks of the lighter colours over the deeper, and in Sweet Peas of the lighter wings over the more fully coloured depends on the fact that in each of these dominants a *reducing* factor is present.

3. *Symbolic Representation of Compositions.*

We may now represent the composition of the varieties mentioned above as :—

Fully-coloured.		*Reduced.*	
STOCKS—			
Terra-cotta	A_1P_1.	Flesh	A_1P_1I.
Crimson	$A_1P_1A_2$.	Rose	$A_1P_1A_2I$.
Theoretical bluish-red variety*	$A_1P_1P_2$.	Lilac	$A_1P_1P_2I$.
Purple	$A_1P_1A_2P_2$.	Pale purple	$A_1P_1A_2P_2I$.
SWEET PEAS—			
Tinged white	A_1P_1.		
Miss Hunt	$A_1P_1A_2$.	Painted Lady,	$A_1P_1A_2I$.
Picotee	$A_1P_1P_2$.		
Purple, purple-winged	$A_1P_1A_2P_2$.	Purple Invincible (viz., blue-winged),	$A_1P_1A_2P_2I$.

The original colour-producing factors C and R of Bateson, Saunders, and Punnett† are represented in the present scheme by the combination $A_1P_1A_2$ and their B factor by the blueing peroxydase P_2.

The activator A_2 represents the factor for uniform colour as contrasted with Picotee; it enables more oxidation, and hence the wings are more intensely coloured.

From this scheme we see that all coloured forms contain one or more oxydase systems, and should give the guaiacum reaction, which is in accordance with the experimental evidence given under Result 1.

Loss of A_1 or P_1 from the plant results in albinism, since A_2P_2 can only act upon the product of the action of A_1P_1.

Hence albinos may contain any of the following combinations of factors :—

$A_1A_2P_2$	(*a*)	A_1	(*h*)
$P_1A_2P_2$	(*b*)	A_2	(*i*)
A_1A_2	(*c*)	P_1	(*j*)
A_1P_2	(*d*)	P_2	(*k*)
P_1A_2	(*e*)		
A_2P_2	(*f*)		
P_1P_2	(*g*)		

Any albino containing A_1 mated with any albino containing P_1 will give a coloured F_1, the class of colour depending on the nature of the other factors present.

Though the activator-peroxydase systems (*a*), (*b*), (*d*), (*e*), and (*f*) are unable to oxidise the plant chromogen, they are nevertheless capable of blueing guaiacum, and this affords an explanation for the experimental results obtained from testing various whites with guaiacum.

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* F_2 from the cross terra-cotta × purple, in which this variety should appear, has not yet been obtained.

† 'Rep. Evol. Com.,' III, p. 3.

In Sweet Peas, for instance, the round- and long-pollened whites producing F_1 purple would be represented as A_2P_1 and A_1P_2 respectively. The round white gives a stronger direct action with guaiacum than the long, as would be expected, since A_2, the factor for uniform colour, is a more powerful activator than A_1, the Picotee factor.

In Stocks, the composition of the cream glabrous and white glabrous giving F_1 purple would be A_2P_1 and $A_1A_2P_2$* respectively; the presence of two activators in the white accounts for its stronger direct action as compared with the cream (Result 3).

We should expect to find all forms of albino (*a*) . . . . . (*k*) among the F_2 whites from the Sweet Pea cross; from the Stock cross, the albinos (*a*), (*b*), (*c*), (*e*), and (*f*). Though differences in the guaiacum reaction could actually be detected among the whites (Results 2 and 3), yet the various combinations could not be identified with certainty in the material available this year, owing to complications due to the presence of other factors not yet considered. It is hoped that further observations will be made next year upon whites of known extraction.

The observations given under Result 4 were less complicated, in that the whites thrown by rose were theoretically of two kinds only, *i.e.* 3 of the composition A_2P_1 : 1 of the composition P_1. Experimentally some individuals were found to give a slight direct and a strong indirect action, others a weaker indirect action in the proportion of 3 strong : 1 weak.

The whites from red (Result 5) were all theoretically of the composition A_2P_1. Experimentally they behaved alike, giving a slight direct and a strong indirect action.

In conclusion, it may be stated that the peroxides X_1 and X_2 have not as yet been identified with any organic substances. P_1 and A_2 have been identified directly with certain guaiacum reactions.

To P_2 and A_1 the tests have only applied indirectly, and the proof of their existence is based rather on analogy with P_1 and A_2 than on direct experimental evidence.

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* A_2 must be common to both parents, since terra-cotta does not appear in F_2.

HYBRIDISATION EXPERIMENTS WITH *MIRABILIS JALAPA.*

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(Received July 6, 1909.)

[Plates 1 and 2.]

Introduction.

Mirabilis Jalapa, "Sweet Marvel of Peru," belongs to the natural order Nyctagineæ, and is, as its name denotes, a native of Peru, and also of other parts of tropical America. It is sometimes known as "Four o'clock," owing to the fact that the flowers open every afternoon about that time. They last through the night, but wither early the following morning. A fresh batch of blossoms appears again that afternoon, and so on day after day throughout the flowering season. This regular habit of putting forth flowers at a definite hour each day, is, however, subject to a certain amount of irregularity during wet or very dull weather.

The flowers are protogynous, and if while they are open pollen is not carried to the stigma by insects or some other agency, when the corolla withers the style coils up and presses the stigma against the stamens in such a way that self-fertilisation is ensured. So effectual is this mechanism, that it is never necessary to fertilise by hand the flowers which one wishes to "self." It is quite sufficient to cover them when in bud and leave them to themselves. Each flower sets but a single seed. The plants are perennial.

The range of colours found in the flowers of the species *M. Jalapa* is wide, and includes various shades of pink, red, and yellow, as well as white forms. Further, almost any combination of these colours may occur, *e.g.* red and white, yellow and white, red and yellow, and even tri-coloured forms; that is to say, white flowers marked with red and yellow.

The colour-markings in these bi- and tri-coloured forms vary very much, ranging from a few small spots or stripes to an area including half or three-quarters of the flower. This phenomenon has throughout the present paper been referred to as "flaking," a term usually applied to the variegated forms of carnations, and used as including spots, splashes, and whole segments of colour, as well as stripes.

It is characteristic of *Mirabilis* that the bi- and tri-coloured individuals almost always produce a few whole-coloured flowers; *e.g.* a plant having most of its flowers white flaked with yellow, bears some pure yellow and some pure white blossoms, and so on.

It may also here be noticed that, in the whole-coloured types, a star-shaped area in the centre of the flower is usually of a slightly different colour from the rest of the corolla. Thus, in the whites it is greenish, in the reds of a more magenta shade, in the yellows of a paler yellow, etc.

Practically all the colour-varieties found at present seem to have been known ever since the plant was introduced into Europe in 1596. Gerard, in his 'Herbal' of 1633, gives an excellent and charming description of them. "This marvellous variety" [of colour, etc.], he says, "does not without cause bring admiration to all that observe it"; and again: "it [the plant] is called in English rather the Marvel of the World than of Peru alone."

Hybridisation experiments with *Mirabilis* have been made at various times by Kölreuter, Gärtner, Naudin, and Lecoq, but the work of these observers consisted principally in crossing together the different species *M. Jalapa*, *M. dichotoma*, and *M. longiflora*. Recently important and detailed experiments in hybridising the various colour varieties of *M. Jalapa* have been made by Correns, and published in 1902 and 1904.* In the first of these papers he gives a short summary of the work of the earlier observers, which may therefore be omitted here.

A discussion of the results obtained by Correns will be given when the present experiments have been fully described.

DETAILS OF THE EXPERIMENTS.

Three colour varieties were used by me, namely, white, crimson, and yellow.† All of these were proved by selfing to be breeding true.

These varieties were then crossed together in various ways. Seven individual whites were used. In many other instances it has been shown that the factorial composition of white-flowered plants may be various, and that, though all may be alike white, some may contain colour-factors absent from others. Such diversity was proved to exist in these *Mirabilis* whites.

By crossing the seven white plants with the same coloured type (yellow), it was found that six of them were alike in composition, and that the seventh, W 7, was distinct. This last case, being the simplest, will be described first.

Case I. *White* (*W* 7) × *Yellow.*

All the F_1 plants from this cross bore flowers of a pale yellow colour (Plate 1, fig. 5).

On selfing these pale yellows, F_2 plants of three kinds were obtained: namely, those bearing flowers of the same colour as the parent types—that is, yellow and white, and also those bearing the pale yellow or heterozygous form. The numbers obtained were in close approximation to the ratio 1 : 1 : 2.

On further selfings, it was found that in the 3rd generation the

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* 'Berichte der Deutschen Botanischen Gesellschaft,' vol. 20; *ibid.*, vol. 23.

† Plate I, figs. 1, 2, 3 and 4.

Table I.—White (W 7) × Yellow, and *vice versâ.*

F_1, 1906.

Parents.	No. of offspring.	Colour.	
(i) W 7 × Y 1	7	Pale yellow.*	
(ii) Y 1 × W 7	3	,,	
(iii) W 7 × Y 2	4	,,	
(iv) Y 2 × W 7	15	,,	
Total.........	29	All pale yellow.	

F_2, 1907.

	No. of plants selfed.	No. of offspring.	Colours.		
			Yellow.	Pale yellow.	White.
Offspring of (i)	2	32	7	15	10
,, (ii)	1	13	5	6	2
,, (iii)	2	26	7	13	6
Total.........	5	71	19	34	18
		Numbers calculated ...	*17·75*	*35·5*	*17·75*

F_3, 1908.

Colour of parent.	No. of plants selfed.	No. of offspring.	Colour of offspring.		
Yellow	4	11	All yellow.		
		Expectation...	.... *All yellow.*		
White	5	11	All white.		
		Expectation...	.... *All white.*		
			Yellow.	Pale yellow.	White.
Pale yellow	6	22	6	11	5
		Numbers calculated ...	*5·5*	*11*	*5·5*

* Sometimes, but only *very* rarely, minute spots, as narrow lines of magenta, were noticed on some of the flowers of these plants, and on the pale yellows of the following generation.

plants resembling the parent types bred true, whilst the pale yellows again broke up in accordance with expectation (*cf.* Table I).

Case II. *White (other than W 7) × Crimson.*

In this cross the flowers of F_1 were of a deep magenta colour, quite distinct from that of the crimson parent (Plate 1, fig. 6).

F_2 from these plants contained crimsons, whites, and the heterozygous magentas in the ratio 1 : 1 : 2.

F_3, raised from them, showed that the crimsons and whites were pure, whilst the magentas broke up as before (*cf.* Table II).

Table II.—White (other than W 7) × Crimson, and *vice versâ.*

F_1, 1905.

Parents.	No. of offspring.	Colour.
(i) W 6 × C 4	2	Magenta.
(ii) C 3 × W 6	7	,,
(iii) W 6 × C 3	6	,,
(iv) C 3 × W 3	4	,,
(v) C 6 × W 3	4	,,
Total	23	All magenta.

F_2, 1906.

	No. of plants selfed.	No. of offspring.	Colours.		
			Crimson.	Magenta.	White.
Offspring of (i)	2	41	9	21	11
	Numbers calculated ...		*10·25*	*20·5*	*10·25*

F_3, 1907.

Colour of parent.	No. of plants selfed.	No. of offspring.	Colour of offspring.		
Crimson	4	38	All crimson.		
		Expectation.	*All crimson.*		
White	3	21	All white.		
		Expectation.	*All white.*		
			Crimson.	Magenta.	White.
Magenta	5	60	14	31	15
	Numbers calculated ...		*15*	*30*	*15*

On crossing back some magenta hybrids of the 1st generation with the white parent, however, an unexpected result was obtained: namely, in addition to whites and magentas, of which there should have been equal numbers, there appeared also whites flaked with magenta. It was noticeable that the flaked and unflaked forms together made up very nearly the expected number of pure whites, of which there was otherwise a very considerable shortage. In accordance with expectation, no crimsons appeared (*cf.* Table III).

Table III.

Parents.	No. of offspring.	Colour of offspring.		
		Magenta.	White, flaked magenta.	White.
(White × crimson) F_1 × white	27	15	8	4
			12	
	Expectation...	*13·5*	*13·5*	

Further, in another cross of white × crimson (using different individuals) a similar shortage of pure whites, and appearance of whites flaked with magenta, was noticed in the 2nd generation, as well as the normal magentas and crimsons.

But in this case the numbers obtained were not satisfactory for evidence, and the experiment has not at present been carried further.

These two cases are, however, interesting in connection with the whole question of "flaking," which will be considered later when dealing with some of the more complicated cases where it again appeared.

Case III. *Yellow* × *Crimson.*

The F_1 flowers from this cross were of an orange-red colour; the star-shaped area in the centre of the flower being, however, of a magenta shade (Plate 2, fig. 7). When selfed they produced F_2 plants bearing yellow, crimson, and orange-red flowers respectively, the numbers being approximately in the ratio 1 : 1 : 2.

Of these plants the yellows and crimsons bred true, whilst the orange-reds again gave all three colours (*cf.* Table IV). The numbers were aberrant, but from the general course of the results it is clear that this departure from expectation had no special significance.

Table IV.—Yellow × Crimson, and *vice versâ*.

F$_1$, 1906.

Parents.	No. of offspring.	Colour.
(i) Y 1 × C 3	6	Orange-red.
(ii) C 3 × Y 1	4	"
(iii) Y 2 × C 3	10	"
(iv) C 3 × Y 2	3	"
(v) C 6 × Y 1	8	"
(vi) C 6 × Y 2	2	"
Total.........	33	All orange-red.

F$_2$, 1907.

	No. of plants selfed.	No. of offspring.	Colours.		
			Yellow.	Orange-red.	Crimson.
Offspring of (iii) ...	2	29	7	16	6
" (iv) ...	1	13	6	3	4
" (v) ...	2	31	6	15	10
Total.........	5	73	19	34	20
	Numbers calculated ...		*18·25*	*36·5*	*18·25*

F$_3$, 1908.

Colour of parent.	No. of plants selfed.	No. of offspring.	Colour of offspring.		
Yellow	7	27	All yellow.		
		Expectation...	.... *All yellow.*		
Crimson	5	29	All crimson.		
		Expectation...	.... *All crimson.*		
			Crimson.	Orange-red.	Yellow.
Orange-red	8	36	10	13	13
	Numbers calculated ...		*9*	*18*	*9*

Case IV. *White* (*W* 7) × *Crimson.*

The results obtained on crossing whites, other than W 7, by crimson have already been given (p. 35, Table II), and it has been stated that W 7 × yellow gave a result different from any of the other whites crossed by that colour. I have now to record the result of crossing W 7 × crimson. This case, though more complicated than any of the three already described, proved a very interesting one.

The flowers of F_1 were of a magenta-rose colour, *i.e.*, of a shade quite distinct from that of the magentas produced on crossing white, other than W 7 × crimson, but one difficult to convey in words (Plate 2, fig. 8).

These plants, on being selfed, produced in F_2 not only the parental and the hybrid forms, *i.e.*, white, crimson, and magenta-rose, but *also* yellows, pale yellows, magentas, and orange-reds (*cf.* Table V).

Table V.—White (W 7) × Crimson, and *vice versâ.*

F_1, 1907 and 1908.			
Parents.	No. of offspring.	Colour.	
(i) W 7 ·6 × C 6 ·1 ...	6	Magenta-rose	
(ii) W 7 ·7 × C 37 ·2...	5	,,	
(iii) C 6 ·5 × W 7 ·6 ...	2	,,	
Total............	13	All magenta-rose	

F_2, 1908.			
	No. of plants selfed.	No. of offspring.	Colour of offspring.
Offspring of (i)	2	37	White. 8 Pale yellow. 3 Yellow. 2 Magenta-rose. 12 Crimson. 2 Orange-red. 4 Magenta. 6

	Pale yellow.	Yellow.	Crimson.	Magenta.	Orange-red.	Magenta-rose.	White.
Numbers calculated	*4 ·6*	*2 ·3*	*2 ·3*	*4 ·6*	*4 ·6*	*9 ·2*	*9 ·2*
Numbers observed.........	3	2	2	6	4	12	8

Of these, the first, *i.e.* yellow, was similar to one of the original type forms (Plate 1, fig. 2), whilst the remaining three resembled *the heterozygous forms of the three simple crosses already described*, namely, the pale yellow from white (W 7) × yellow (Table I), the magenta from white (other than W 7) × crimson (Table II), and the orange-red from yellow × crimson (Table IV) (*cf.* Plate 1, figs. 5, 6, and 7).*

Before attempting to account for this result I will describe the next case, white (other than W 7) × yellow, where the same forms again occur, but with the further complication that "flaking" also appeared.

Case V. *White (other than W 7) × Yellow.*

The F_1 plants from this cross bore flowers of a magenta-rose colour, similar to that obtained when W 7 was crossed by crimson (*cf.* p. 38). The majority were, however, further "flaked" with orange-red, though, as is usual in these forms, some unflaked blossoms were also found (Plate 2, fig. 9).

Table VI.—White (other than W 7) × Yellow, and *vice versâ.*

F_1, 1905 and 1906.

Parents.	No. of offspring.	Colour of offspring.
(i) Y 3 × W 6	2	Magenta-rose, flaked orange-red.
(ii) Y 3 × W 4	2	,, ,, ,,
(iii) Y 1 × W 6	1	,, ,, ,,
(iv) Y 3 × W 3	1	,, ,, ,,
(v) Y 1 × W 4	1	,, ,, ,,
(vi) W 1 × Y 2	8	,, ,, ,,
(vii) W 2 × Y 1	8	,, ,, ,,
(viii) Y 1 × W 1	4	,, ,, ,,
(ix) W 2 × Y 2	4	,, ,, ,,
(x) Y 2 × W 2	8	,, ,, ,,
(xi) W 2 × Y 4	3	,, ,, ,,
(xii) W 5 × Y 4	4	{ 2 ,, ,, ,, { 2 white, flaked with magenta.†
(xiii) W 5 × Y 1	3	Magenta-rose, flaked orange-red.
(xiv) Y 2 × W 5	3	,, ,, ,,
(xv) W 1 × Y 1	3	,, ,, ,,
Total	55	{ 53 magenta, rose, flaked orange-red. { †2 white, flaked magenta.

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* See dated Note at end of paper.

† These two plants were accounted for by finding that Y 4 was not breeding true, but throwing white, flaked with yellow, as well as pure yellow plants; it was, therefore, not used again.

In the next generation, besides the parent and hybrid forms, *i.e.* white, yellow, and magenta-rose flaked with orange-red (and a few similarly-coloured but apparently completely unflaked plants), *six* other forms appeared, viz., crimson, magenta, orange-red, pale yellow (pure or flaked with darker yellow), white flaked with yellow, and white flaked with magenta (Plate 2, figs. 10, 11, and 12).

Here, as in the last case, we have the appearance of a form similar to one of the types originally used, *i.e.*, crimson, also of the three heterozygous forms, magenta, orange-red, and pale yellow, and finally of the two new white flaked forms.

On selfing all these various plants the following results were obtained :—

The *whites*, *yellows*, and *crimsons* all bred perfectly true, being apparently, as one would expect, homozygous (Table VIII (i), (ii), and (iii)).

The *orange-reds* gave, as in the case where they were produced from the simple cross yellow × crimson (*cf.* Table IV), yellows, crimsons, and orange-reds in a ratio very fairly in accordance with expectation. (Table VIII (iv).)

The *magentas* gave, as in the case where they were produced from the cross white (not W 7) × crimson (*cf.* Table II), crimsons, magentas, whites, and also whites flaked with magenta, the two latter classes together making up as before (*cf.* p. 36) almost exactly the expected number of *pure* whites. (Table VIII (v).)

The *pale yellows*, as when produced from crossing W 7 × yellow (*cf.* Table I), gave yellows, pale yellows, whites, and, in addition, whites flaked with yellow, the latter appearing, as in the last case, largely to take the place of *pure* whites. (Table VIII (vi).)

The *whites flaked with yellow* gave a majority of plants similar to themselves, but also some which bore only pure yellow, and others only pure white flowers. As regards the former, it was not always easy to decide whether they should be classed as yellows or pale yellows ; but this was probably owing to the fact that these particular plants proved rather a stunted set and were late in flowering, in which case the various shades of colour are often difficult to distinguish. (Table VIII (vii).)

The *whites flaked with magenta** differ in regard to their composition as do the pure whites (*cf.* p. 33).

Thus of the four plants selfed, one gave only whites flaked with magentas and whites flaked with yellow, two others gave almost the

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* Such flaked whites should strictly be distinguished according as the flakes of colour are magenta or magenta-rose ; but in practice this discrimination is scarcely possible. The latter only can throw forms in which yellow appears, being heterozygous in M. For simplicity these various classes are spoken of collectively as whites flaked with magenta.

Table VII.—White (other than W 7) × Yellow, and *vice versâ*.

F_2, 1906, 1907, and 1908.

	No. of plants selfed.	No. of offspring.	Crimson.	Magenta.	Orange-red.	Yellow.	Pale yellow, flaked and unflaked.	Magenta-rose, flaked and unflaked.	White, flaked magenta.	White.	White, flaked yellow.
Offspring of (i) ...	2	40	1	1	3	6	3	11	6	3	6
,, (ii) ...	2	24	7	3	4	—	1	2	4	2	1
,, (iii) ...	1	2	—	—	—	—	—	—	1	—	1
,, (iv) ...	1	11	—	3	—	—	2	2	3	—	1
,, (v) ...	1	2	—	—	—	1	1	—	—	—	—
,, (vi) ...	3	100	14	13	16	4	11	22	10	6	4
,, (x) ...	2	74	6	9	12	3	13	24	4	2	1
,, (vii) ...	2	70	7	13	6	7	9	15	7	3	3
,, (x) ...	1	40	4	3	11	2	5	7	4	1	3
,, (i) ...	1	43	4	6	8	2	5	7	7	2	2
,, (ii) ...	1	41	2	6	5	2	6	11	3	3	3
Total	17	447	45	57	65	27	56	101	49	22	25
										96	
Numbers calculated			*28*	*56*	*56*	*28*	*56*	*112*		*112*	

whole range of colours, whilst the fourth gave only crimsons, magentas, whites, and whites flaked with magenta. (Table VIII (viii).)

The *magenta-roses flaked with orange-red* gave the whole colour series as before, the calculated and observed ratios coinciding very fairly, especially as the numbers dealt with were comparatively small. (Table VIII (x).)

Finally, two of the similar but *unflaked* magenta-roses gave all the *whole*-coloured types (except pale yellow, which would very probably have appeared if more plants had been raised), but no flaked ones, just as in the case of the 2nd generation from the cross W 7 × crimson. The numbers obtained were, however, too small to allow of working out the ratios satisfactorily. (Table VIII (ix).)

Explanation of Results from the Crosses W 7 × Crimson and White (other than W 7) × Yellow.

Having now given the details of these two crosses, *i.e.* white (W 7) × crimson, and white (other than W 7) × yellow, where a number of forms are produced in the 2nd generation, a consideration of the probable colour-factors involved may be attempted. For the present only *self-coloured* types will be discussed.

The factors, in accordance with the views of Correns, may be taken as consisting of two pairs, namely :—

$$^{*}\ \text{I}\begin{cases} \text{C} = \text{the factor for } \textit{coloured} \text{ sap.} \\ \text{c} = \text{absence of this factor.} \end{cases}$$

$$\text{II}\begin{cases} \text{M} = \text{a factor which turns yellow sap } \textit{red.} \\ \text{m} = \text{absence of this factor.} \end{cases}$$

Then if we consider first the composition of the white types, that of W 7 must = cm, for since it is white, the sap is colourless, and it cannot contain C; and again, since when crossed with yellow it gave a *pale yellow* (not red) hybrid, it cannot contain M.

The composition of the remaining six whites, on the other hand, must = cM, since *all*, when crossed with yellow, give *red* hybrids (*cf.* Table VI).

Finally, the composition of the crimson and yellow types must then be CM and Cm respectively.

We will next consider the composition of the heterozygous forms obtained from the three simple crosses of these types.

That of the pale yellow must be Ccmm, since it results from crossing white (W 7 = cm) × yellow (= Cm).

Again, that of the magenta must be CcMM, since it is obtained by crossing white (*not* W 7 = cM) × crimson (= CM).

$$^{*}\ \textit{Cf.}\ \text{I}\begin{cases} \text{F} = \text{Farbstoff.} \\ \text{kF} = \text{kein Farbstoff.} \end{cases} \quad \text{II}\left.\begin{cases} \text{M} = \text{Modifikation in Rot} \\ \text{kM} = \text{kein Modifikation in Rot} \end{cases}\right\} \text{of Correns.}$$

F$_3$, 1907 and 1908.

Colour of F$_2$ parent.	No. of plants selfed.	No. of offspring.	Colour of offspring.
(i) Yellow	4	52	All yellow. Expectation ,,
(ii) Crimson	4	49	All crimson. Expectation ,,
(iii) White	5	14	All white. Expectation ,,
(iv) Orange-red	4	59	18 yellow, 28 orange-red, 13 crimson. Numbers calculated *14·75* ,, *29·5* ,, *14·75* ,,
(v) Magenta	4	54	13 crimson, 26 magenta, $\underbrace{\text{12 white-flaked magenta, 3 white.}}_{15}$ Numbers calculated *13·5* ,, *27* ,, *13·5*
(vi) Pale yellow	3	47	8 yellow, 21 pale yellow, $\underbrace{\text{13 white-flaked yellow, 2 white.}}_{15}$ Numbers calculated *11·75* ,, *23·5* ,, *11·75*
(vii) White-flaked yellow	4	64	16 white, 34 white-flaked yellow, 14 yellow (or pale yellow).
(viii) White-flaked magenta—			
α	1	24	α 19 white-flaked magenta, 5 white-flaked yellow.
β	1	11	β 2 white, 6 white-flaked magenta, 2 magenta, 2 crimson.
γ	2	32	γ 10 white-flaked magenta, 5 white-flaked yellow, 5 white, 4 pale yellow. 2 orange-red, 4 magenta-rose, 2 magenta.
(ix) Magenta-rose (unflaked)	2	19	4 white, 2 crimson, 6 magenta, 4 orange-red, 2 yellow, 1 magenta-rose.
(x) Magenta-rose, flaked orange-red	3	48	4 crimson, 8 magenta, 4 orange-red, 11 magenta-rose (flaked and unflaked). Numbers calculated *3* ,, *6* ,, *6* ,, *12* ,, ,, ,, 2 yellow, 9 pale yellow (flaked and unflaked), $\underbrace{\text{3 white-flaked magenta, 4 white, 3 white-flaked yellow.}}_{10}$ *3* ,, *6* ,, *12*

Finally, that of the orange-red must be CCMm, since it results from crossing yellow (= Cm) × crimson (CM).

We may now turn to the details of the cross white (W7) × crimson. Here, since W 7 = cm and crimson = CM, the F_1 must = CcMm.

The following diagram, then, shows the complex composition of the 2nd generation, and accounts satisfactorily for the appearance of the yellow type (CCmm), and also of the three heterozygous forms: pale yellow = Ccmm, magenta = CcMM, and orange-red = CCMm.

Diagram showing the Composition of F_2 from the Cross White (W 7) = cm × Crimson = CM.

Crimson. CM CM	Magenta. cM CM	Orange-red. Cm CM	Magenta-rose. cm CM
Magenta. CM cM	White. cM cM	Magenta-rose. Cm cM	White. cm cM
Orange-red. CM Cm	Magenta-rose. cM Cm	Yellow. Cm Cm	Pale Yellow. cm Cm
Magenta-rose. CM cm	White. cM cm	Pale Yellow. Cm cm	White. cm cm

Composition of F_2.	Magenta-rose.	Magenta.	Orange-red.	Pale yellow.	Crimson.	Yellow.	White.
Numbers calculated	9·2	4·6	4·6	4·6	2·3	2·3	9·2
Numbers obtained	12	6	4	3	2	2	8

Moreover, the calculated and observed ratios, in accordance with these schemes of colour-factors, correspond very fairly.

If we next consider the cross white (other than W 7) × yellow, we find that F_1 is again CcMm, since white = cM and yellow = Cm.

The 2nd generation from this cross should therefore produce a similar colour series to that obtained in the 2nd generation of the cross W 7 × crimson, and if for the moment we neglect "flaking" and include the white-flaked forms with the *pure* whites, this is actually found to be the case.

The diagram already given, therefore, serves again, and the calculated and observed numbers are as follows:

Composition of F_2 when flaked forms appear.	Magenta-rose, flaked and unflaked.	Magenta.	Orange-red.	Pale yellow, flaked and unflaked.	Crimson.	Yellow.	White.		
							Flaked magenta.	Flaked yellow.	Unflaked.
Numbers calculated	*112*	*56*	*56*	*56*	*28*	*28*	*112*		
Numbers observed	101	57	65	56	45	27	49	25	22
							96		

Further, the 3rd generation from this cross has been raised* (*cf.* p. 40), and if we here again neglect the "flaking," which will be referred to later, the results obtained are in accordance with expectation from the scheme of colour-factors proposed (*cf.* p. 42 and Table VIII).

The following evidence may also be adduced in favour of this scheme. It is seen from the diagram that the whites, extracted in the 2nd generation, though they will, of course, all appear similar, should really be of different constitutions. Whether this was actually the case or not could, however, only be proved by crossing them all with the same coloured form, *e.g.*, yellow.

This was accordingly done, with the following result: Of the five white-flowered plants tested, four were evidently of the composition ccMm, for they all gave *both* magenta-rose flowers flaked with orange-red and pale yellow flowers flaked with darker yellow. The combined numbers of the two colours from the four plants proved, in accordance with expectation, almost equal.

The fifth plant was, however, in all probability of the composition ccmm, since it gave *only* pale yellow flowers flaked with darker yellow.

It will be noticed that "flaking" proved dominant throughout.

Further experiment with other F_2 whites from this cross would in all probability have revealed some having the composition ccMM, which, indeed, was that of the six whites used in the original cross (*cf.* Table VI).

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* The 3rd generation from the cross W 7 × crimson is being raised this year (see dated note at end of paper).

Table IX.—Extracted Whites (F_2) from (Whites × Yellow) × Yellow.

	No. of offspring.	Colour of offspring.	
		Magenta-rose (flaked).	Pale yellow (flaked).
α	3	1	2
β	8	5	3
γ	10	5	5
δ	10	6	4
Total	31	17	14
*Calculated numbers		...............*15·5*	*15·5*
ε	8	All pale yellow (flaked).	
*Expectation.....................		.... *All pale yellow.*	

* The assumption being that α, β, γ and δ are of the composition ccMm, and ε of the composition ccmm.

Case VI. *White* (*W* 7) × (*other*) *Whites.*

This cross proved of great interest, and although it has not as yet been fully worked out, it seems worth while to give the results so far obtained, since they furnish another example of two whites crossed together being able to produce coloured forms (*cf.* Sweet Peas, etc.).

Of the plants of the 1st generation—13 in number—12 bore white flowers flaked with magenta-rose (Plate 2, fig. 10), the 13th had flowers of the magenta-rose *self-colour* (Plate 2, fig. 8).

In the next generation, of which only 22 plants have at present been raised, whites, whites flaked with magenta, whites flaked with yellow, and one pale yellow *self-colour* appeared.*

Now, according to the scheme of colour factors already set forth (p. 42), W 7 = cm, and the other whites = cM. If we further assume that, as in the case of the sweet peas,† two factors are necessary for the production of colour, then it is possible that one of these whites—say W 7—contains one factor, the other whites the other. This would account for the production of a coloured F_1, the "flaking" being brought in here, as elsewhere, by the whites other than W 7.

And here, too, might possibly lie some clue to the shortage of pure whites and the appearance of the white flaked forms in the 2nd generation of the cross white × yellow. But further speculation on this point is idle until more evidence has been obtained.

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* A larger number of F_2's, and also the F_3 generation, are being raised this year.

† Third Report to the Evolution Committee, p. 3.

Table X.—White (W 7) × various Whites.

F$_1$, 1907 and 1908.

Parents.	No. of offspring.	Colour.
(i) W 7 × W	3	All white, flaked magenta.
(ii) W 7 × W	3	2 white, flaked magenta. 1 magenta-rose.
(iii) W 7 × W	7	All white, flaked magenta.
Total	13	12 white, flaked magenta. 1 magenta-rose.

F$_2$, 1908.

	No. of plants selfed.	No. of offspring.	Colour of offspring.			
			White.	White, flaked magenta.	White, flaked yellow.	Pale yellow.
Offspring of (i)	3	22	11	7	3	1

It may, however, be added that on crossing together any other two of the original six whites used, pure whites only were obtained.

Table XI.—Whites (other than W 7) crossed together.

F$_1$, 1907.

Parents.	No. of offspring.	Colour.
(i) W 2 × W 5	4	White.
(ii) W 3 × W 1	4	,,
(iii) W 6 × W 4	3	,,
Total	11	All white.

Conclusion, and Comparison with Correns' Results.

The most important points of the experiments described above in detail are, I think, the following:—

(i) The discovery of a white form (W 7), which, when crossed by yellow, gave in F$_1$ pale yellow (not red) hybrids (*cf.* p. 33), and therefore appears to be the one predicted by Correns in the following sentence:

"eine (nicht hybride) *alba*-Sippe existieren könnte, die mit einer gelben bestäubt, *gelbe* Bastarde geben würde."

(ii) The fact that this white (W 7), when crossed by *crimson*, gave in F_2 practically the same series of coloured forms as was obtained when any other white was crossed by *yellow*, but uncomplicated by "flaking" (*cf.* "Streifung" of Correns), which occurs in the latter case (pp. 38 and 39).

(iii) The discovery that this white (W 7), when crossed by other whites, produced coloured forms (p. 46).

(iv) The fact that the heterozygous forms are always distinct in colour from any homozygous types.

(v) When the heterozygous forms are properly distinguished, the inter-relationships of the F_2 series are evidently those shown in the table (p. 44), and this analysis is complete so far as these self-coloured forms are concerned. The scheme given by Correns (1904, p. 80) needs considerable modification, for in it the visible distinction between the heterozygous terms is not recognised,* and several terms are indicated as possible which cannot actually be formed.

Correns was the first to discover that white crossed by yellow gave the striking magenta-rose hybrids flaked with orange-red ("hell rosa, mit roten Sprenkeln and Streifen") (*cf.*, p. 39), and he set forth the scheme of colour-factors which accounted for their appearance, and which I have employed in the present paper (p. 42).

But since he apparently never made the cross yellow × crimson, which gives the characteristic orange-red hybrids, nor happened to discover a white similar to W 7 which when crossed by yellow gives a pale yellow, he could not recognise these heterozygous forms when they appeared again in F_2 from white × yellow. Further, though he seems to have made the cross white × crimson, he makes no note of any distinct shade of colour (*i.e.* magenta) appearing in F_1, nor of having recognised it again in F_2 from white × yellow.

Struck by the unexpected result of the latter cross, *i.e.*, the appearance of "red" flowers, Correns directed his attention principally to unravelling the composition of the numerous forms which appeared in the 2nd generation unaided by the clue which a study of the simple cases, coupled with the fortunate discovery of W 7, appears in the present set of experiments to have provided.

(vi) As regards the "flaking," it seems to me, at present at any rate, impossible to give any satisfactory explanation of it, although many attempts have been made, and one cannot help feeling that there

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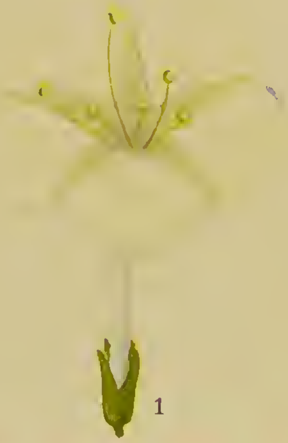
* In a later paper ("Über Vererbungsgesetze," Berlin, 1905, p. 19) he notes the distinction between crimson and the magenta-rose heterozygote, but his figure on p. 27 represents a *pale* yellow as a pure type. Such plants, in my experience, are always heterozygous in C. The homozygous yellow is the deep yellow which Correns represents in the F_2 series.

PLATE 1.



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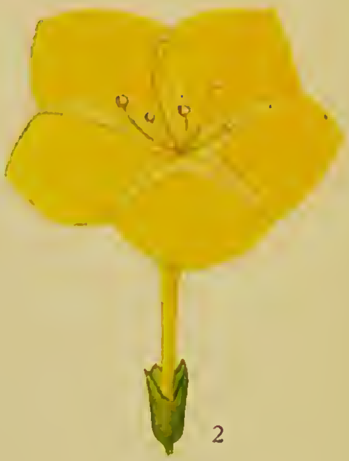

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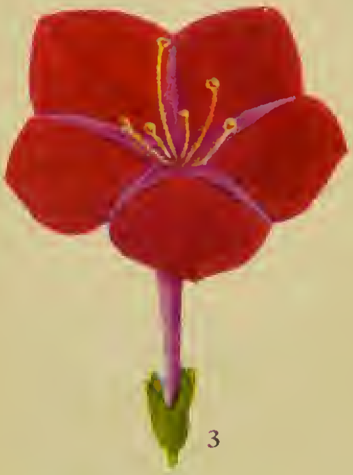

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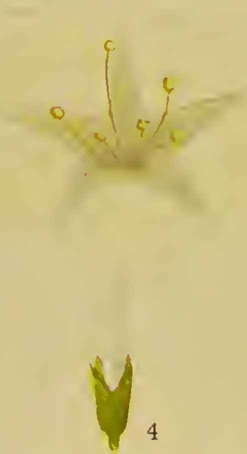

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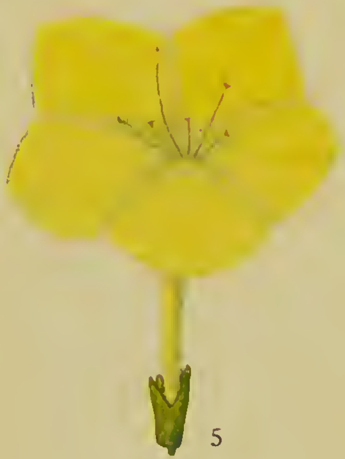

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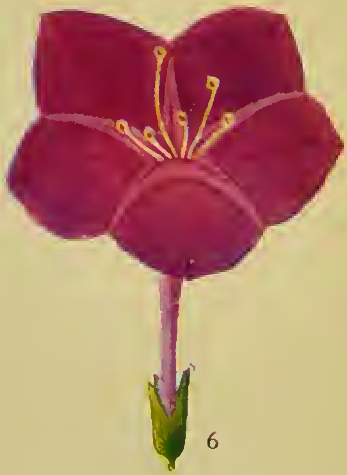


6

1. White (W7) (*Type*)
[cc mm].

2. Yellow (*Type*)
[CC mm].

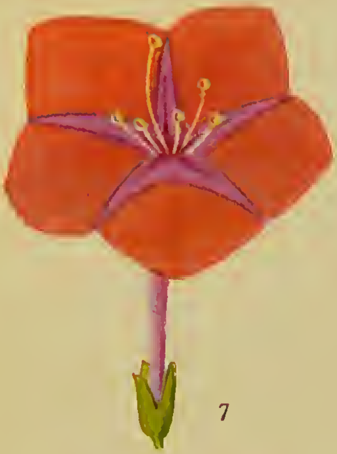
3. Crimson (*Type*)
[CC MM].

4. White (*Type*)
[cc MM].

5. Pale Yellow—F1 from 1 × 2
[Cc mm].

6. Magenta—F1 from 4 × 3
[Cc MM].

PLATE II.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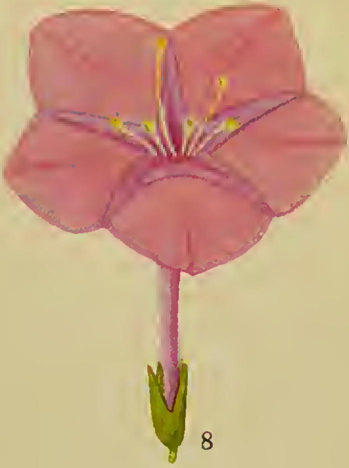
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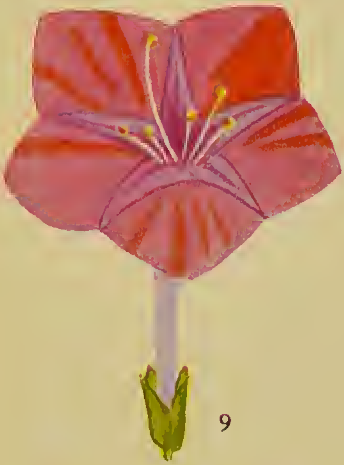
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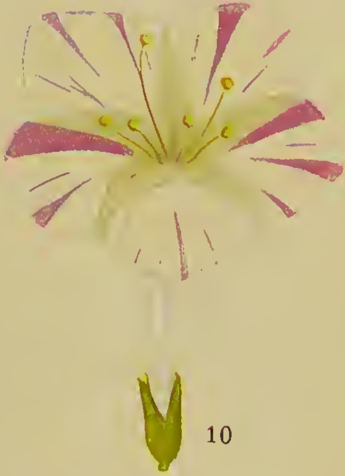
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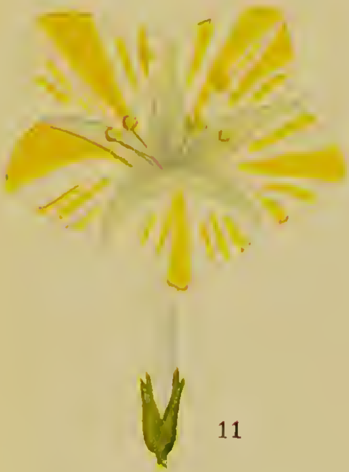
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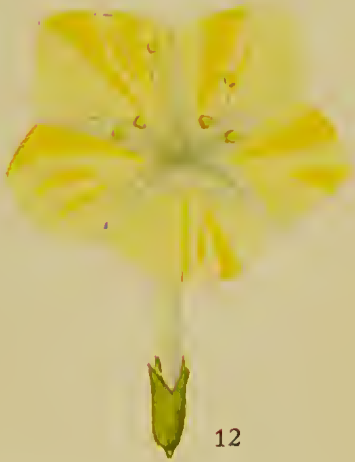
12

7. Orange-red—F1 from 2 × 3
[CC Mm].

8. Magenta-rose—F1 from 1 × 3
[Cc Mm].

9. Magenta-rose, flaked Orange-red—
F1 from 4 × 2
[Cc Mm]

10. White, flaked Magenta—F1 from 1 × 4.
Appears also in F2 from 4 × 2.
[cc Mm].

11. White, flaked Yellow
Appears in F2 from 4 × 2.

12. Pale Yellow, flaked Yellow.
Appears in F2 from 4 × 2.

is a certain orderliness about the phenomenon. For if the white flaked forms are added to the pure whites, as was done on p. 41, it is striking how nearly the calculated and observed numbers coincide. Again, in the other cases where white-flaked as well as pure whites occur, the two combined always seem to make up approximately the expected number of *pure* whites, of which there is otherwise a quite unaccountable shortage (Table VIII, (v) and (vi), etc.).

It may further be pointed out that in the cases where there was no complication from "flaking," the correct number of pure whites was always approximately obtained (*cf.*, Tables I, V, and XII).

The essential difficulty is that we cannot yet propose a simple factorial scheme which will represent consistently the three facts—(1) that F_1 from white × self-colour may be flaked with yellow pigment (on a coloured ground, such flakes appearing orange-red); (2) that F_2 from such a cross contains whites *as* 1 *in* 16, *instead of as* 1 *in* 4 which is the ratio when no flaked forms occur; (3) that though flaked forms occasionally throw self-coloured individuals, this phenomenon is so irregular that its significance is quite uncertain. In the course of this work no tricolour flowers (*i.e.*, those having both red and yellow flakes) have been met with, and it is not impossible that by a study of their behaviour a solution may be found.

One thing at least seems clear, namely, that the "flaking" is introduced by the whites (other than W 7), as Correns also concluded, and since it has been shown that white (W 7) × white (any other) can give white forms flaked with colour, it is possible that further experiments in this direction may throw some light upon the matter.

At present it does not seem possible to consider "flaking" and its "absence," as a pair of simple Mendelian factors, for although several elaborate schemes have been worked out along these lines, none of them have proved satisfactory. And in spite of the fact that one is left with the feeling that there surely must be some clue to this phenomenon, it must frankly be acknowledged that, up to the present, the clue has not been found.

Correns endeavoured to elucidate the matter, but he, too, found it a difficult problem; and after having hit upon a satisfactory explanation of the reason why "red" forms appeared when white was crossed by yellow, he remarks: "Viel weniger befriedigend steht es mit der Erklärung der neuauftretenden Streifung."

In conclusion, I wish to express my gratitude to Professor Bateson for his kind help and advice throughout these experiments and during the writing of this paper. I am greatly indebted to Miss Wheldale, who has kindly prepared the coloured plate. I also wish to offer my thanks to Mr. Lynch, both for allowing me to use the original *Mirabilis* plants growing in the Cambridge Botanical Gardens and for his care and assistance in the raising of the seedlings.

[*Note added September*, 1909.—Since this paper was communicated, F_3 from W7 × crimson (see p. 38) has been raised, and proved in accordance with expectation, *i.e.*, the crimsons and yellows both bred true, the magentas broke up into crimsons, whites, and magentas; the orange-reds into crimsons, yellows, and orange-reds; and the pale yellows into yellows, whites, and pale yellows; whilst the magenta-roses, like the F_1, gave again the whole colour series. The agreement between the calculated and observed ratios proved, on the whole, very satisfactory (Table XII); and here, where there is no complication from "flaking," an adequate number of pure whites was obtained in each case (see Table XII, iv, v, and vi, and *cp.* p. 41).]

Table XII.—White (W7) × Crimson.

F_3, 1909.

Colour of parent.	No. of plants selfed.	No. of offspring.	Colour of offspring.
(i) Yellow	2	26	All yellow. *All yellow.*
(ii) Crimson	2	23	All crimson. *All crimson.*
(iii) Orange-red ...	3	61	15 yellow, 31 orange-red, 17 crimson. *15·75* „ *31·5* „ *15·75* „
(iv) Magenta	4	64	14 white, 32 magenta, 18 crimson. *16* „ *32* „ *16* „
(v) Pale yellow ...	3	46	12 white, 25 pale yellow, 9 yellow. *11·5* „ *23* „ *11·5* „
(vi) Magenta-rose	5	70	21 white, 3 yellow, 7 pale yellow, 5 crimson. *17·25* „ *4·37* „ *8·75* „ *4·37* „ 9 magenta, 6 orange-red, 19 magenta-rose. *8·75* „ *8·75* „ *17·25* „

Expectations in *italics*.

DESCRIPTION OF PLATES.

The coloured figures are reproductions of diagrammatic drawings kindly made by Miss Wheldale. On the whole they represent the colours fairly well. It should be noted that the sharpness of the central "star" is exaggerated, and, except in the whites, it shades off gradually into the substance of the petals. In flaked flowers this "star" is not necessarily free from flaking (as represented in the figures), but more commonly is flaked like the rest of the petals. Moreover, fig. 12 exaggerates the distinctness with which the yellow flaking appears.

An attempt has been made to record the colours by means of the *Répertoire de Couleurs*, published by the Soc. Franç. des Chrysanthémistes et René Oberthür, which has been recommended to horticulturists.

Yellow (fig. 2) is Jaune d'Auréoline	Plate 22, Shade 3.
Pale yellow (fig. 5) is ditto	Plate 22, Shade 1.
Crimson (fig. 3) is Fuchsine..	Plate 160, Shade 4.
Magenta (fig. 6) is nearly Magenta rougeâtre	Plate 169, Shade 2.
Magenta-rose (fig. 8) is Pourpre de Tyr	Plate 155, Shade 2.
Orange-red (fig. 7) agrees imperfectly with Rouge Framboise...	Plate 117, Shade 3.

INHERITANCE OF COLOUR AND OF SUPERNUMERARY MAMMÆ IN GUINEA-PIGS, WITH A NOTE ON THE OCCURRENCE OF A DWARF FORM.

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(Received July 6, 1909.)

[PLATE 3.]

The present paper is a statement of the facts which have been obtained by experimental crossing of the colour varieties of guinea-pigs during the years 1903–1908. The scheme of colour factors which has been constructed from the qualitative results of these crosses (see p. 55) gives an expectation of quantitative results which differ somewhat from the numbers actually obtained. Hence, for the present, this scheme can only be regarded as tentative, and the problem of the gametic constitution of the colour varieties of guinea-pigs is not completely solved. The greatest deviation of the obtained from the expected totals will be found on p. 64.

In guinea-pigs the colour varieties fall into two main divisions characterised the one by a dark eye, the other by a ruby eye. The dark eye varies in density of pigmentation, but it always contains some black pigment. The ruby eye contains chocolate pigment only, and its colour is likewise variable in intensity. The two groups form corresponding series, as shown below; the types in each series are epistatic to those beneath them in the column :—

Dark-eyed series.		Ruby-eyed series.	
Dense.	Dilute.	Dense.	Dilute.
Agouti	Yellow- and silver-agouti.	Cinnamon	Yellow- and silver-cinnamon.
Black	So-called "blue."	Chocolate	Silver-fawn.
Red	Yellow and cream.	Red	Yellow and cream.

Agouti.—The hair of the agouti guinea-pig, like that of other agouti animals, possesses alternate bands of black and red pigment. This arrangement is known in the fancy as "ticking." Usually the entire coat is ticked, but even in pure bred agoutis patches of unticked, uniformly red hair may occur. In hybrids derived from the cross agouti × red these unticked patches may be of considerable extent, but as far as my experience goes the number of red offspring produced by mating two uniformly ticked hybrids *inter se* does not differ from the number resulting from matings of hybrids bearing red patches. Beneath every such red unticked patch the skin has only a trace of the black pigment present in the skin beneath the ticked hairs. It seems clear that the occurrence of these unticked patches is due not to any want of continuity in the distribution of the factor which determines ticking, but rather to a discontinuity in the distribution of the dark pigment which makes possible the manifestation of the presence of the ticking factor. This statement is based on the facts that *black* patches never occur in agouti animals, and that red patches do occur in black animals.

The skin, like the eye, of the agouti contains black pigment which is densest in the ears, feet, and nose.

Black.—Black animals contain a very variable amount of red pigment in the coat. Pure blacks, which are prized in the fancy, give among their offspring some which are like themselves, but a larger number bearing red patches of greater or less extent. In hybrid blacks derived from the red × black cross there is a gradation from a coat which is black save for a few red hairs, to one which is red save for a few black hairs. The extremes* are less common than the intermediate types, but all appear to be similar in their hereditary properties. As far as I know, two pure black animals mated together do not produce young bearing red patches of large size such as occur in the hybrids. The skin and eye of the black guinea-pig contain black pigment which is very dense in the eye and in the skin of the ears and feet.

Red, dark-eyed animals possess only red pigment in the hairs. The chief skin pigment is chocolate, but a trace of red and of black pigment can also be detected.

In these three dark-eyed types the living eye, even when examined in bright light, has a brown iris and a black pupil, while in the ruby-eyed types, described later, the iris is light brown and the pupil ruby coloured in bright light. With very little practice it becomes easy to detect the difference between these two types of eye even in moderate daylight.

Cinnamon.—This type may be described as agouti without the black pigment. The hairs are ticked with bands of chocolate and red pigment. Red patches without chocolate pigment, and consequently without ticking, may occur just as red patches occur in the agouti, but a cinnamon with chocolate patches is unknown. I first obtained the cinnamon variety by mating together (January 18, 1909) agouti F_1 from the cross chocolate by dark-eyed red. The skin contains chocolate and red pigment.

Chocolate.—This breed was first obtained by Mr. Roberts, of the National Cavy Club, in 1904. The hairs are chocolate with a variable amount of red or cream pigment patches. The same statements which I have made above concerning the red patches of blacks are true of the red or cream patches in this breed. The skin contains chocolate and red pigment.

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* Blacks whose hairs are almost all red are exceedingly rare, and are easily distinguishable from true reds.

Red, ruby-eyed animals possess only red pigment in the hairs. In the skin the chief pigment is red, but a trace of chocolate occurs in the deeper layers of the skin. I first obtained this breed by mating together (September 17, 1906) F_1 agoutis from the cross dark-eyed red × chocolate, but it can, of course, be bred in various other ways.

This type, which has a red coat and a red skin with a trace of chocolate and a ruby eye, is the lowest term in the series of coloured types; all the others are epistatic to it.

Albinos entirely free from pigment are, as is well known, the exception among guinea-pigs. As soon as the chocolate race was established by Mr. Roberts in 1904, it became obvious that the chief ear-pigment of albinos carrying chocolate was chocolate, while the points of albinos obtained from any of the old dark-eyed breeds contained black pigment.* Later, the cinnamon breed appeared, and the ears, etc., of their albinos were likewise chocolate. Finally, in the points of albinos carrying ruby-eyed red or cream the chief pigment is red.

Dilution.—At present I am not able to deal in detail with dilute colours, as further experiments are necessary. Each colour exists not merely in the dense form and a dilute form, but in a large number of dilute forms shading into one another and into the dense form. It remains to be seen how this is to be expressed by means of factors. As far as my experience goes, two reds, or two creams, or two yellows mated together, never give young darker than either parent. In the chocolate breed the chocolate and the red patches of the same animal have not necessarily the same density. Also in self-coloured animals the colour may have a different density in different parts of the body; indeed, certain parts of the face in the dilute breeds of any colour are commonly darker than the rest of the body either throughout life or during adolescence.

The dilute shades of black are known as "blue" in the fancy, but it is not the same colour which is called blue in mice; it has much the appearance which we might imagine that a chocolate guinea-pig would have if we could add a little black pigment to the coat. A very dilute black is not at once distinguished from the dense chocolate by an observer unaccustomed to these colours, but the hairs are strikingly different when examined microscopically. Also the skin colour forms a marked distinction, being black in the dilute black and chocolate in chocolate, and again the eye is dark in the dilute black, ruby in the chocolate. The difference in the appearance of the dilute black in guinea-pigs and of the blue in mice may be, I believe, due to the difference in the arrangement of the pigment particles (fig. 1).

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* See Castle, 'Science,' 1908, p. 251.

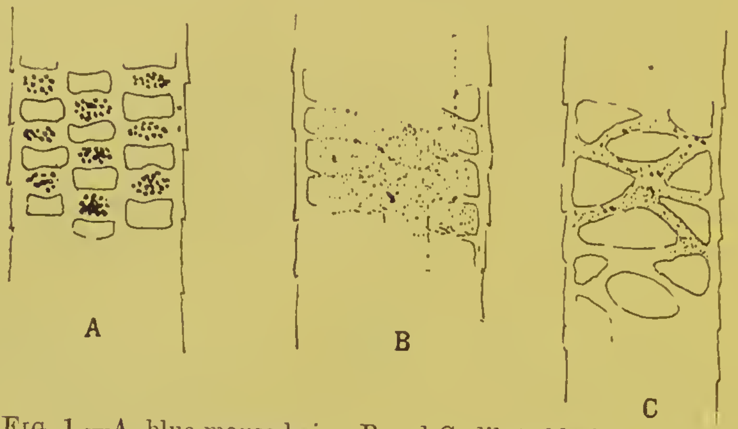

Fig. 1.—A, blue mouse hair ; B and C, dilute black Cavy hair. (B, general impression ; C, optical section).

Scheme of Gametic Factors.

Not only are the qualitative results of all the crosses that have yet been made consistent with the following scheme of gametic factors, but when this scheme was first drawn up the results in generations F_1 and F_2 of the cross black × ruby-eyed red were unknown, and were correctly predicted from it. It still remains to be seen what the F_2 generation of the cross agouti × chocolate will be: there need be no hesitation in foretelling that it would consist of agoutis, cinnamons, blacks, and chocolates.* The letters used in the scheme have the following significance :—

G	a factor determining	ticking of the hairs.
B	,, ,,	black pigment in the eye and skin.
R	,, ,,	red pigment in the hair, and red and chocolate pigment in the skin and eye.
Ch	,, ,,	chocolate pigment in the hair, skin, and eye.
C	,, ,,	colour.

[The small letters denote the absence of the factor represented by the corresponding large letters.]

The albinos have the same gametic formula as the colour variety from which they are extracted, except for the absence of C. It is clear that, as the albino guinea-pig has coloured points, the absence of C in this case cannot be complete.

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* Since this was written, Prof. Castle has made this cross with the above results, 'Science,' 1908, p. 251.

Colour varieties.	Factors.				
	G	B	R	Ch	C
Agouti	×	×	×	×	×
Black	—	×	×	×	×
Red, dark-eyed		×	×	—	×
Cinnamon	×	—	×	×	×
Chocolate	—	—	×	×	×
Red, ruby-eyed		—	×	—	×
Albino carrying black	—	×	×	×	—
,, ,, chocolate	—	—	×	×	—
,, ,, red, dark-eyed		×	×	—	—
,, ,, ,, ruby-eyed		—	×	—	—

CROSSES.

1. *Coloured Types* × *Albinos.*

Seeing that the albino guinea-pig differs from most albino animals in possessing some pigment, the question naturally arises whether among the descendants of the offspring of crosses of albino and coloured guinea-pigs the proportion of coloured animals to albinos is that which is usual. The evidence so far obtained seems to show that it is. Albinism is recessive to colour, and the offspring of coloured hybrids carrying recessive albinism, when mated with albinos, are coloured animals and albinos in approximately equal numbers. Thus out of 383 young resulting from crosses of this nature, 197 were coloured and 186 were albinos. The separate totals are these :—

Colour of coloured parent.	Offspring.	
	Coloured.	Albino.
Agouti	70	70
Black	12	9
Red, dark-eyed	12	11
Cinnamon	10	4
Chocolate	59	53
Silver agouti	1	5
Dilute black	3	6
Cream, dark-eyed	25	21
Cream, ruby-eyed	5	7
Total	197	186

2. *Coloured Types × Coloured Types.*

When the various colour varieties are crossed together a certain amount of blending is perceptible in the offspring, but this is not sufficient to mask the dominance. The results of the various crosses are discussed below.

Generation F_1.—Agouti crossed by any other colour gives agouti offspring only; when the other colour is black the offspring are generally darker than the agouti parent; this darker agouti is preferred by some fanciers, and black is crossed in purposely; hence, it is important to test carefully the agouti stock used for crosses. When the other colour is red, there are frequently red, unticked patches in the coat of the offspring.

	Parents.		Offspring.	Gametic factors (neglecting dilution).
Cross 1......	Agouti.	Black.	Agouti.	
	10 ♀	18 ♂	4	Agouti, GBRChC.
	11 ♀	18 ♂	6	Black, gBRChC.
		Total	10	
Cross 2......	Agouti.	Red (or cream).	Agouti.	
	11 ♀	271 ♂ red	5	Red, $^{G}_{g}$BRchC. The two cream ♂ ♂ 251 and 233 carry recessive albinism, so that half their gametes will be $^{G}_{g}$BRchc.
	11 ♀	288 ♂ ,,	2	
	145 ♀	14 ♂ ,,	6	
	147 ♀	14 ♂ ,,	7	
	10 ♀	128 ♂ cream	2	
	10 ♀	251 ♂ ,,	7	
	10 ♀	233 ♂ ,,	3	
		Total	32	
Cross 3......	Agouti.	Chocolate.	Agouti.	
	147 ♀	134 ♂	5	Chocolate, gbRCh.

Black and chocolate alike, when crossed with dark-eyed red, give either agouti or black young. A weaker pigmentation is noticeable in the offspring from the red × chocolate cross when they are compared with those from the red × black cross. It can be shown that the factors G and g which determine whether the offspring shall be black or agouti are carried by the red parent.*

	Parents.			Offspring.	Gametic factors.
Cross 4......	Red.	Black.	Chocolate.	Black.	
	241 ♀	18 ♂		4	Red, pure, gBRchC. Black, pure, gBRChC. Chocolate, carrying recessive albinism, gbRChC and gbRChc.
	241 ♀		143 ♂	10	
	241 ♀		232 ♂	6	
	170 ♀	18 ♂		11	
	170 ♀		232 ♂	3	
			Total......	34	

The same black and chocolate individuals which, as shown in the above table, when mated with certain reds gave black only, when mated with other reds gave both black and agouti young, thus—

	Parents.			Offspring.		Gametic factors.
Cross 5...	Red.	Black.	Chocolate.	Black.	Agouti.	
	15 ♀	18 ♂		8	7	Red { GBRchC. gBRchC. Black, gBRChC. Chocolate, carrying albinism, gbRChC and gbRChc.
	15 ♀		143 ♂	1	1	
			Totals......	9	8	

Thus 15 ♀ was heterozygous in G, and probably possessed equal numbers of gametes containing G and g, while 241 ♀ and 170 ♀, which have given respectively 20 and 14 black young in matings with blacks and chocolates, are probably homozygous in g. A red male, 14 ♂, was apparently homozygous in G.

Crosses 7 and 8 are similar to crosses 4 and 5, and point to the same conclusions. They differ chiefly in that the pigmentation of the red parent is dilute instead of dense.

Thus 233 was heterozygous in G; of 34 gametes, 12 carried G 22g. Apparently 211 was homozygous in g, as perhaps also were 251, 256, 257. I do not happen to have had any cream homozygous in G.

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* This was stated by Castle in 'Science,' 1907, but his evidence was not published

Just as in the dark-eyed series, agouti is epistatic to black and red (as well as to the whole of the ruby-eyed series), so in the ruby-eyed series cinnamon is epistatic to chocolate and ruby-eyed red.

	Parents.				Offspring.	
Cross 6...	Red.	Black.	Chocolate.	Albino determining dilute black.	Agouti.	Gametic factors.
	14 ♂	12 ♀			9	Red, GBRchC. Black, gBRchC. Chocolate, gbRChC. Albino determining black, gBRChc.
	14 ♂	13 ♀			4	
	14 ♂		142 ♀		2	
	14 ♂			64 ♀	5	
	14 ♂			206 ♀	3	
				Total...	23	

	Parents.			Offspring.			
Cross 7...	Cream.	Black.	Chocolate.	Agouti.	Black.	Albino.*	Gametic factors (neglecting dilution).
	233 ♂	250 ♀		6	5		233 ♂ carried recessive albinism: the gametes were therefore GBRchC, gBRchC, GBRchc, gBRchc. The chocolate ♀ ♀ also carried recessive albinism, gbRChC and gbRChc.
	233 ♂	249 ♀			3		
	233 ♂	240 ♀		3	2		
	233 ♂	78 ♀		2	1		
	233 ♂		208*a* ♀ (dilute)		2 (dilute)		
	233 ♂		261 ♀		2 (dilute)		
	233 ♂		279 ♀		1 (dilute)	1	
	233 ♂		209 ♀	1	6 (dilute)	2	
			Totals......	12	22		

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* Albinos will be found among the offspring in many of the tables; but their presence does not affect the relative numbers of the various coloured young, and is neglected.

When crossed with black or dark-eyed red, cinnamon gives agouti. Ruby-eyed red crossed with chocolate gives cinnamon or chocolate or both, and again it can be shown that it is the nature of the gametes of the red parent which determines between these alternatives.

	Parents.			Offspring.		Gametic factors.
Cross 8...	Cream.	Black.	Chocolate.	Black.	Albino.	
		Dense or dilute.	Dilute.	Dense or dilute.		
	211 ♂	249 ♀		3		All the creams carried recessive albinism. Their gametes were gBRchC and gBRchc. Similarly some of the chocolates carried recessive albinism, gbRChC and gbRChc. Black, pure, gBRChC, except in the case of 236 ♀, which also had gBRChc.
	211 ♂	240 ♀		3		
	211 ♂	236 ♀		4		
	211 ♂	13 ♀		7		
	251 ♂	236 ♀		9	1	
	256 ♀		143 ♂	2		
	256 ♀		273 ♂	1	1	
	256 ♀		329 ♂	4		
	257 ♀		134 ♂	3		
	257 ♀		273 ♂	4		
	Total coloured......			40		

	Parents.		Offspring.		Gametic factors.
Cross 9...	Red, ruby-eyed.	Chocolate.	Cinnamon.	Albino.	
	312 ♂	279 ♀	8		GbRchC, gbRChC, GbRchc, gbRChc.
	314 ♀	309 ♂	2	1	
	369 ♂	220 ♀	8		

Thus 312 and 369 may have been homozygous in G, but the numbers are too small to justify a definite conclusion.

	Parents.		Offspring.			Gametic factors.
Cross 10.	Cream, ruby-eyed.	Chocolate.	Cinnamon.	Chocolate.	Albino.	
	427 ♂	261 ♀	1 (golden)	1	1	${}^{G}_{g}$bRch${}^{C}_{c}$ and gbRCh${}^{C}_{c}$.
	427 ♂	261 ♀	3 (yellow)			
	427 ♂	433 ♀	1 (golden)	1		

As was to be expected, the same cream which, when crossed with chocolate, gives cinnamon and chocolate, when crossed with black gives agouti and black, seeing that Cross 10 shows that it is heterozygous in G, g.

	Parents.		Offspring.		Gametic factors.
Cross 11...	Cream, ruby-eyed.	Black.	Agouti.	Black.	
	427 ♂	240 ♀	2		${}^{G}_{g}bRch^{C}_{c}$ and gBRChC.
	427 ♂	250 ♀		3	

I have not yet had any examples of ruby-eyed reds or creams homozygous in g, but I have chocolates which, when mated together, give some chocolate and some red or cream offspring, and these red or cream offspring, if tested, would doubtless prove to be homozygous in g.

Parents.		Offspring.	
Chocolate.	Chocolate.	Chocolate.	Red.
320 ♀	333 ♂	6	1

The colours of the offspring in the second filial generation, F_2 of these various crosses will now be considered.

Cross 1.—Agouti × Black.

Parents.		Offspring F_2.	
F_1 agoutis.		Agouti.	Black.
196 ♀	197 ♂	4	2
198 ♀	197 ♂	8	2
199 ♀	197 ♂	16	3
Totals		28	7
Expectation ...		26·25	8·75

Cross 2.—Agouti × Red or Cream dark-eyed.

(*a*) Agouti 11 ♀ × cream 128 ♂

290 agouti ♀ (F_1) × 288 red ♂

2 black 1 red 1 agouti.

The male 128 was known to carry g, for 128 ♂ × 240 black ♀ gave four black offspring. Had it been otherwise (*i.e.*, had 128 carried G only) we should not expect any black offspring on crossing the agoutis of generation F_1 with red or cream. The male 288 was also carrying g, but may have been heterozygous in G, g.

The gametes of 290 will be GBRCh, gBRCh, GBRch, gBRch. When each of these meet the gametes of 288 they will give agoutis, blacks, reds carrying Gg and reds carrying gg—that is, young in the proportion of one agouti, one black to two red, if 288 is homozygous in g.

(*b*) Agouti 145 ♀ × cream 233 ♂ heterozygous in G, g

289 agouti F_1 ♀ × 233 ♂

1 yellow agouti, 3 silver agouti, 1 black-red, 1 black-cream, 3 red

or neglecting dilution 4 agouti, 2 black, 3 red.

The male 233 was heterozygous in G, g; therefore the young obtained from it on crossing with an F_1 agouti carrying black would be 3 agouti to 1 black to 4 red.

Any F_1 agouti crossed with a red homozygous in G would give equal numbers of agouti and red young.

Cross 3.—Agouti × chocolate (GBRChC × gbRChC).

I have not reared any of these. Agoutis from this cross, mated together, would give young in the proportions 9 agoutis, 3 black, 3 cinnamon, 1 chocolate. Castle* states that he has obtained F_2 offspring from this cross, his numbers being 8 agouti, 4 black, 2 cinnamon, and 2 chocolate.

Cross 5 (*a*).—Red dark-eyed × Black, giving Agouti.

The gametes of the agoutis of generation F_1 from the cross black × red will be :—GBRChC, GBRchC, gBRChC, gBRchC. Therefore the offspring expected in F_2 will be agoutis, blacks, and reds in the proportions 9 : 3 : 4.

There is thus an excess of reds and a deficiency of blacks, but in the case of the family from 54 × 55 the proportions are nearly those expected.

Castle† adopts a gametic formula which differs from that which is used in this paper, but which nevertheless, in this particular case of the red by black crosses, gives an expectation of the same proportionate numbers of agouti, red, and black young in F_2. He states

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* 'Science,' 1908, p. 251.

† 'Science,' 1907, p. 151.

Parents.	Offspring.			
F_1 agoutis from the cross black × red.	Agouti.	Black.	Red.	Albino.
148 ♀ 149 ♂	15	4	10	
179 ♀ 180 ♂	13	2	10	
54 ♀ 55 ♂	21	6	9	
F_1 agoutis from the cross black × cream.				
410 ♀ 411 ♂	9		5	
447 ♀ 411 ♂	5	1	1	
516 ♀ 543 ♂	1		2	
516 ♀ 523 ♂	2	1		
522 ♀ 523 ♂	3		3	
447 ♀ 543 ♂	3		5	4
Totals obtained	72	14	45	—
Expectation	73 ·6775	24 ·5625	32 ·75	

that he has obtained the expected numbers in F_2, and in some cases in F_3, but he does not quote his numbers, which would be very welcome. He states that F_1 agoutis, when mated *inter se*, produce agouti, black and red young in the proportions 9 : 3 : 4, and that when mated with reds they produce 1 agouti to 1 black to 2 reds.

But he does not mention a fact (see p. 61) which is clearly important, viz., that the colours of the offspring produced by the cross of F_1 agoutis with reds depends upon whether the red is carrying his factor A (= G) or not. Thus, if the red is not carrying G, then the numbers will be, as he says, 1 agouti, 1 black, 2 red; but if it is homozygous in G there will be equal numbers of reds and agoutis, and if it is heterozygous (Gg), 3 agoutis, 1 black, 4 red. Among the animals he tested he found that red carrying g was comparatively rare, so that the chances are in favour of his having used reds homozygous in g for the cross in question. My own experience in respect to the rareness of the factor G in reds, does not agree with Castle's, but rather suggests, what might have been expected, that reds bought from one fancier agree among themselves, and differ from those of another fancier, in the possession or lack of this factor.

Of the F_2 agoutis I have obtained very little information so far. Castle states that they fall into four classes :—

(1) Agoutis, like their parents, giving offspring when mated *inter se* in the proportions 9 agouti, 3 black, 4 red. Gametic constitution R,AB, forming gametes R,RA, B,BA, where R is a factor determining red pigment, B, black, and A, ticking.

(2) Agoutis which when mated with reds produce agoutis and reds in equal proportions; gametic constitution RA,BA forming gametes, RA,BA with equal frequency.

(3) Agoutis which when mated with reds produce no red offspring, but only agoutis and blacks with equal frequency, gametic formula BA,B forming gametes BA,B with equal frequency.

(4) Expected class: agoutis which breed true BA,BA.

Now, it would seem to me that numbers which were sufficient to establish the existence of the first three classes should also be sufficient to determine whether or not the fourth class exists, though it must be remembered that the fourth class would be the rarest. Of every 9 F_2 agoutis, 4 would belong to Class 1, 2 to Class 2, 2 to Class 3, and 1 to Class 4.

The question whether the red mate is carrying A (G) or not is again important in Classes 1, 2, 3. For if an agouti of Class 1 is mated with a red carrying A, the young will be agoutis and reds in equal numbers, and this class will be indistinguishable from Class 2. In Class 3, if the red mate is carrying A, the young will be all agoutis, and this class will be indistinguishable from Class 4.

My own numbers are not sufficient to be of use in determining the gametic constitution of the F_2 agoutis. They are as follows :—

1. Matings of Agoutis with Reds.

Parents.		Offspring.		
F_2 agouti.	Red.	Agouti.	Black.	Red.
268	270	1		2
268	271	3	2	1
269	270	6		9
435	394	3		
403	602	3	1	
517	406	1		1
517	257	2		1
517	595	4		4
517	422	1		1

2. Matings *inter se* of F_2 Agoutis.

		Agouti.	Black.	Red.
402 × 403	gave	10	3	7
575 × 576		1	1	
268 × 267		1	1	
435 × 466		3		3
435 × 466		2		2
552 × 605		2		

Now, if the expectation 9 agoutis, 3 black, 4 red is correct in the generation F_2, it is correct also for F_3 derived from those of the F_2 agoutis which give offspring of these three colours. Therefore we can add together the totals obtained in F_2 and those in F_3 where all three colours have been obtained.

	Agouti.	Black.	Red.
Offspring of F_1 agoutis (p. 62)	72	14	45
,, F_2 ,, (p. 64)	10	3	7
Totals	82	17	52
Expectation	84 ·9375	28 ·3125	37 ·75

Thus, the excess of reds over the expected number and the deficiency of blacks are maintained, and are of quite formidable size, but the proportion of agoutis to the blacks and reds taken together agrees very nearly with the expectation.

Cross 5 (*b*).—The black F_1 offspring of the cross Black × Red, when mated *inter se*, give black and red young.

Parents.		Offspring.	
Black.	Black.	Black.	Red.
177 ♀	178 ♂	13	1
468 ♀	467 ♂	4	1
Totals		17	2
Expectation.........		15 ·75	5 ·25

To these we may add, if we neglect dilution, the offspring of the black F_1 individuals from the cross black × cream.

Parents.		Offspring.	
Black.	Black.	Black.	Red or cream.
420	421	8	
293	294	15	4
293	467*	3	1
	Total	26	5
	Previous total......	17	2
	Totals	43	7
	Expectation..........	36	12

There is thus a deficiency of reds.

The offspring of the black individuals of F_2 would, theoretically, be of two kinds, viz., blacks breeding true and blacks throwing blacks and reds in the proportion 3 : 1 when mated *inter se*.

Hence to the foregoing totals the following results of mating a black F_2 ♀ with a black F_1 ♂ may be added :—

131 ♀ × 178 ♂ gave 8 black, 6 red.

The total is now 50 black : 13 red where the expectation is 47·25 : 15·75. The deficiency of reds is thus considerably diminished.

Cross 5 (*c*).—Dark-eyed Red × Chocolate giving Agouti.

Seeing that the gametes in the original cross were GBRchC, gbRChC or RC(GBch × gbCh) the gametes of the hybrids will be, in F_1: RC(GBch, gBch, Gbch, gbch, GbCh, gbCh, GBCh, gBCh.) Hence, in F_2 the expectation is: 27 agouti, 9 black, 9 cinnamon, 3 chocolate, 9 dark-eyed red carrying G, 3 dark-eyed red carrying g, 3 ruby-eyed red carrying G, 1 ruby-eyed red carrying g. Or, 27 agouti, 9 black, 9 cinnamon, 3 chocolate, 12 dark-eyed red, 4 ruby-eyed red.

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* 467 was actually from black × *red*. The other parents represented in this table were from black × cream.

The numbers actually obtained are shown in the following table :—

Parents.	Offspring.						
F_1 agoutis.	Agouti.	Black.	Cinnamon.	Chocolate.	Red, dark-eyed.	Red, ruby-eyed.	(Albino.)
438 × 439	2			1	1		2
438 × 379	6	3	1			2	
378 × 379	4	1	2	1	3	3	
520 × 521	12	1		4	2	1	
365 × 366	7	3	5	1	4		6
278 × 154	2	1					
Totals …	33	9	8	7	10	6	(8)

Cross 5 (*d*).—Red × Chocolate giving Black.

In this case the gametes of the original cross were gBRchC × gbRChC or gRC(Bch × bCh), and the gametes of the hybrids will be gR(BCh, bCh, Bch, bch), and the offspring expected will be 9 black, 3 chocolate, 3 dark-eyed red, 1 ruby-eyed red.

Parents.		Offspring, neglecting dilution.				
Black F_1 from chocolate × red.		Black.	Chocolate.	Dark-eyed red.	Ruby-eyed red.	(Albino.)
315	330	11	3	2	1	
338	336	12	5	2	3	
Totals……		23	8	8		
Black, denser or dilute F_1 from chocolate × cream.		Black.	Chocolate.	Red, neglecting eye-colour.		
94	344	10	5	3		8
204	67	17	4	5		
205	67	11	2	2		6
480	481	8	1	1		
480	344	1	1	2		
592	67	1		1		1
593	67	1				
592	481	1		1		
Totals……		50	13	15		

Taking these two sets of totals together, we have, neglecting dilution, 73 black, 21 chocolate, 23 red, where the expectation was 65·8125 : 21·9375 : 29·25. The deficiency of reds recalls that in the cross black by red.

Cross 9 (*a*).—Red or Cream, ruby-eyed × Chocolate, giving Cinnamon.

Parents.	Offspring.			
F_1 cinnamon.	Cinnamon.	Chocolate.	Red.	Albino.
413 × 416	3	2	2	
414 × 416	2		1	1
415 × 416	4	1	3	
487 × 489	5	4	5	
488 × 489	3	1	1	
502 × 503	8	4	2	3
506 × 503	4		2	
414 × 550			3	
572 × 416		2		
586 × 416	1		2	
Totals	30	14	21	
Expectation ...	36·5625	12·1875	16·25	

In discussing the cross dark-eyed red by black, giving agouti in F_1, it was found that theoretically it ought to be possible to obtain in F_2 some agoutis breeding true. I have not made a sufficient number of experiments to determine whether or not this expectation is realised, but I have made an attempt to find an answer to the parallel question whether a cinnamon breeding true can be obtained in F_2 or later generations from the cross chocolate by red. I have tested 24 cinnamons, both parents of which were ticked, *i.e.*, either agouti or cinnamon. The parents were obtained in a variety of ways, in most cases not from a direct cross of ruby-eyed red by chocolate. Of the 24 tested, 20 have been shown to carry either red or chocolate, or both. The remaining 4 have behaved as follows :—

(1) 97 ♀ was produced as shown beneath—

220 ♀, chocolate, × 217 ♂, red, dark-eyed
|
agouti 278 ♀ × 262 ♂ chocolate
|
130 agouti ♀ × 106 cinnamon ♂
|
97 ♀.

This cinnamon has thrown 25 young, all cinnamon. Of these, 3 were the offspring of a cinnamon ♂ 347, known to carry both red and chocolate; 4 the offspring of cinnamon ♂ 323, known to carry chocolate; and 18 of ruby-eyed red ♂ 312.

(2) 381 died after throwing 5 cinnamon young to a cinnamon known to carry red.

(3) 425 died after throwing 1 cinnamon young to a cinnamon 347 ♂.

(4) 372 was produced thus :—

278 ♀ agouti × 262 chocolate ♂
(see under (1)) |
97 ♀ × 323 cinnamon ♂
(see under (1)) |
372 cinnamon ♀ .

This female has thrown 19 young, all of which are some shade of cinnamon: 6 of these were the offspring of a silver cinnamon boar 424, known to carry chocolate and cream, the remaining 13 of a chocolate boar 273.

Thus, of these four, the evidence furnished by two only is of any value at all. It is to be regretted that these two cinnamons were not obtained directly as F_2 from the red by chocolate cross.

In estimating the value of the evidence obtained from these 24 cinnamons, the fact that animals often throw long runs of one colour must not be neglected. Thus, for example, 179 and 180 were agoutis of generation F_1, derived from a red × black cross. They threw 6 red and 11 agouti young before they threw any blacks at all; then came a litter of 2 reds and 1 black; thus there was 1 black in 20 where 3 in 16 was expected. So that it is still possible, though perhaps improbable, that 97 or 372 may yet throw either chocolate or red. On the other hand, those cinnamons which have already thrown either chocolate or red, but not both, may indirectly furnish proof of the possibility of obtaining a cinnamon which breeds true. Thus 113 ♂ is a silver cinnamon which seems from evidence given below to carry chocolate but not cream. Now, this boar gives some cinnamon when mated with chocolate; but if none of its gametes are cream, then its cinnamon offspring are presumably formed from a cinnamon gamete (GbRChC) which, if it met its like, would give a cinnamon breeding true :—

	Agouti.	Cinnamon.	Chocolate.	Albino.
113 ♂ × 5 cream ♀ ♀ gave	7	8	7	6
113 ♂ × 1 chocolate ♀		2		1
113 ♂ × 2 cinnamon ♀ ♀		11	2	3

Cross 12.—Black × ruby-eyed, Red, or Cream.

This cross had not been made at the time that the scheme of gametic factors was drawn up. It is clear that, according to the scheme, the expectation in F_1 would be agoutis and blacks, and in F_2 derived from mating black individuals of generation F_1 *inter se*, blacks, chocolates, dark- and ruby-eyed reds; while in F_2 derived from mating agouti

Parents.	Offspring.				
Blacks from ruby-eyed red or cream × black.	Black.	Chocolate.	Red, dark-eyed.	Red, ruby-eyed.	Albino.
F_1, 525 ♀ × 527 ♂ ,, 526 ♀ × 527 ♂	8	5	1	1	1
,, 531 ♀ × 532 ♂	5		1		3
F_2, 573 ♀ × 574 ♂	6		2	1	
Totals	19	5	4	2	
Expected proportions ...	9	3	3	1	

Parents.		Offspring (neglecting dilution).				
Black from black × ruby-eyed red or cream.	Ruby-eyed red or cream.	Black.	Chocolate.	Dark-eyed red.	Ruby-eyed red.	Albino.
484 ♂	485 ♀	1	1	3	1	
491 ♂	359 ♀	6	1		1	
515 ♂	464 ♀	2	3	3	3	
515 ♂	537 ♀		1			
515 ♂	524bis ♀		1	1	1	
515 ♂	464 ♀			1	1	
526 ♀	555 ♂		1		1	
538 ♂	537 ♀	1	2			1
541 ♂	524 ♀	1	3	3		8
527 ♂	557 ♀				2	
527 ♂	359 ♀		1		1	1
542 ♂	476 ♀	2		1	1	
515 ♂	314 ♀		1		2	
541 ♂	563 ♀	1	3		1	
Totals...............		14	18	12	15	
Expectation		Equal totals.				

individuals of generation F_1 *inter se* there would be agoutis, blacks, cinnamons, chocolates, dark-eyed and ruby-eyed reds. If, instead of mating the blacks of F_1 *inter se* we mate them with ruby-eyed red carrying g, we shall get the above-mentioned colours in equal numbers, viz., blacks, chocolates, dark- and ruby-eyed reds. The actual numbers obtained are given in the two preceding tables.

If we mate the F_1 agoutis of this cross with red or cream, the result depends on whether or not the red or cream carries G or g or both. If it carries g, the offspring will be equal numbers of agoutis, blacks, cinnamons, chocolates, dark-eyed reds heterozygous in Gg, dark-eyed reds homozygous in g, ruby-eyed reds heterozygous in Gg, and ruby-eyed reds homozygous in g. If it is not known whether the reds carry G or g, the results of this cross still have value if we deal with the sum of the agoutis and blacks and the sum of the cinnamons and chocolates:—

Parents (neglecting dilution).		Offspring (neglecting dilution).						
Agouti F_1 from black × ruby-eyed red.	Ruby-eyed red.	Agouti.	Black.	Cinnamon.	Chocolate.	Red, dark-eyed.	Red, ruby-eyed.	(Albino.)
483 ♂	374 ♀	1	1			1	3	2
483 ♂	524 ♀		1		1	1		
483 ♂	601 ♀			1			1	
490 ♀	427 ♂			2	1			
545 ♂	492 ♀		1			1	1	
560 ♀	394 ♂	1						
Total …………		2	3	3	2			
Totals …………		5		5		3	5	
Expectation……		Equal totals.						

Supernumerary Mammæ.

A fairly large number of the guinea-pigs which I have bred have possessed one or two mammæ in addition to the normal inguinal pair.

Relationship between the original individuals showing this feature cannot be proved, though it is quite possible that it exists, in some remote degree, as all of them have some of the blood of Roberts' chocolate stock. All these original individuals were bred from normal stock.

The supernumerary mammæ exist in every grade of development, from a mere bare circular skin-patch, lying in the mammary line, on one side only, to a pair of complete and functional mammary glands with their teats. They occur in males as well as in females. When unpaired, the supernumerary mamma is more often on the left side than on the right. I have never yet obtained animals having more than one pair of supernumerary mammæ. Mr. Graham Bell's* results with sheep led me to expect such animals among the offspring of parents each of which had an extra pair.

The heredity of supernumerary mamma resembles that of extra toe in guinea-pigs and fowls. It does not show either clear dominance or recession. It arises in the offspring of normal parents, and when two animals possessing the character are mated together they bear young some of which are normal while others have one or two supernumerary mammæ. So far, the facts are not inconsistent with dominance of the abnormal character. But this character can pass over a generation, the normal young of abnormal parents giving again abnormal young, and thus in these cases it appears to be recessive.

It is interesting to note that though, as already stated, there are many incomplete stages in which supernumerary mamma may exist, yet the complete stage may be reached, at one step, in the offspring of normal parents.

The following tables show the number of young having supernumerary mammæ and the position of these mammæ: (1) when both

Parents.		Young.			
(1) Both parents with supernumerary mammæ, B on both sides, L on the left side, R on the right side.		Supernumerary mammæ on			
		Left side.	Right side.	Both sides.	Neither side.
♀	♂				
598B	599B			2 ♀ 1 ♂	1 ♀
454B	570B				1 ♀ 1 ♂
454B	455L	1 ♀	1 ♀	2 ♀ 1 ♂	5 ♀ 6 ♂
454B	554R	1 ♂		1 ♀	3 ♂
569 bis B	554R	1 ♀		1 ♂	
365L	366B	1 ♀ 1 ♂		1 ♀ 1 ♂	3 ♀ 5 ♂
535R	536B			1 ♀	1 ♀

In this table it is noticeable that in the columns of young having extra mammæ there are twice as many females as males (11 ♀ : 6 ♂), while in the column of normal young there are more males than females; but in the total number of offspring the numbers of males and females are equal (22 ♀ · 21 ♂).

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* 'Science,' 1899, p. 637, 1904, p. 767, and 'Sheep Catalogue of Beinn Bhreagh, Victoria, co. Nova Scotia, 1904,' and 'Multinippled Sheep of Beinn Bhreagh living 1903 and their known Ancestors, 1904.'

Parents.		Young.			
		Supernumerary mammæ on			
(2) ♀ with supernumerary mammæ on left side.	♂ normal.	Left side.	Right side.	Both sides.	Neither side.
161	245	1♀			3♀
454	211	1♂			1♂
546	236				1♂
546	232			1♀	3♂
364	262				
364	232	1♀	1♀	1♀	3♀ 3♂
458	113				5♀ 4♂
458	113				1♀ 1♂
(3) ♀ with supernumerary mammæ on right side.	♂ normal.				
406	232				6♀ 1♂
205	67				7♀ 8♂
374	18				2♀ 1♂
374	483				2♀ 2♂
(4) ♀ with supernumerary mammæ on both sides	♂ normal.				
407	408	1♂			2♀ 2♂
407	427				3♀ 1♂
352	423				1♀ 2♂
422	232				1♀
422	423	1♀ 1♂			1♀ 6♂
398	426				3 ? sex
398	213				
398	351				4♂
204	67	1♂		1♀ 1♂	3♀ 7♂

parents have one or more of these structures; (2) when a female with supernumerary mamma is mated with a normal male. Circular bare skin-patches on the mammary line are reckoned as supernumerary mammæ.

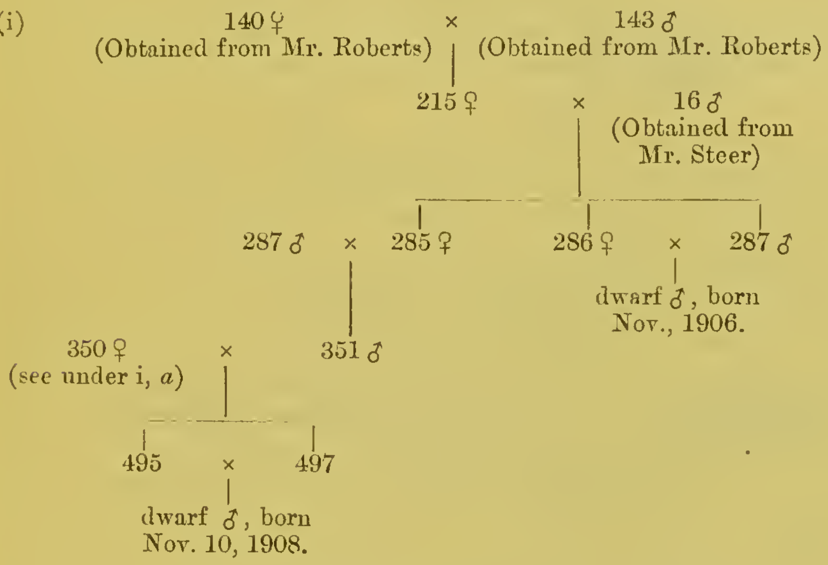
On the Occurrence of a Dwarf Form of the Guinea-pig.

The variation which is described below occurred in the first instance in some of the offspring of apparently perfectly normal guinea-pigs. It is remarkable, because it affects not one part or organ only, but the entire framework of the animal. Differences in form and proportion are accompanied by marked diminution in size and weight as compared with the normal guinea-pig; hence we can, for the sake of shortness, speak of this "sport" as a dwarf.

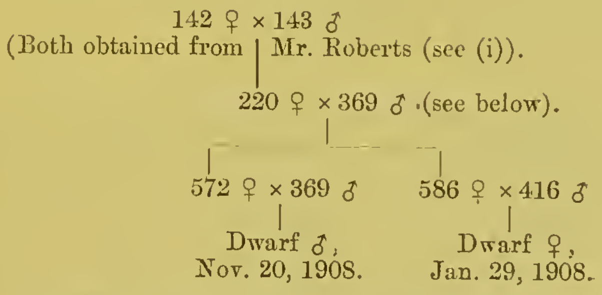
Dwarf offspring have appeared in two families which are, as far as I know, unrelated. Some of the ancestors of these two families were, however, obtained from the same fancier, so that there is a possibility, indeed a probability, of remote relationship. Some of the descendants of both of these families have given some dwarfs among their offspring.

Descent.—The actual details of descent are as follows:—

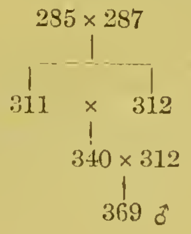
(i)


140 ♀ × 143 ♂
(Obtained from Mr. Roberts)
(Obtained from Mr. Roberts)
215 ♀ × 16 ♂
(Obtained from Mr. Steer)
287 ♂ × 285 ♀
286 ♀ × 287 ♂
dwarf ♂, born Nov., 1906.
350 ♀ (see under i, *a*) × 351 ♂
495 × 497
dwarf ♂, born Nov. 10, 1908.

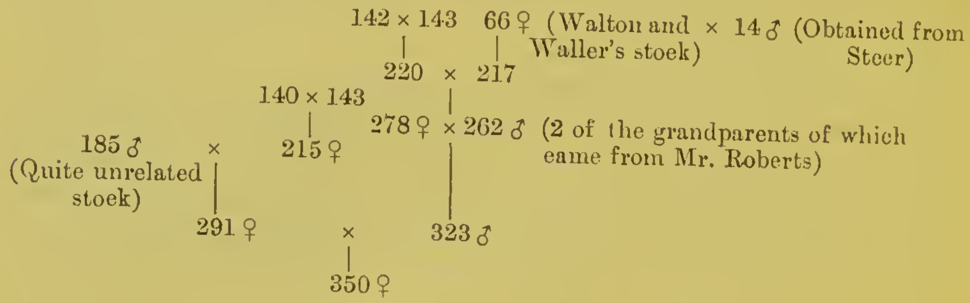
(i, *a*.)



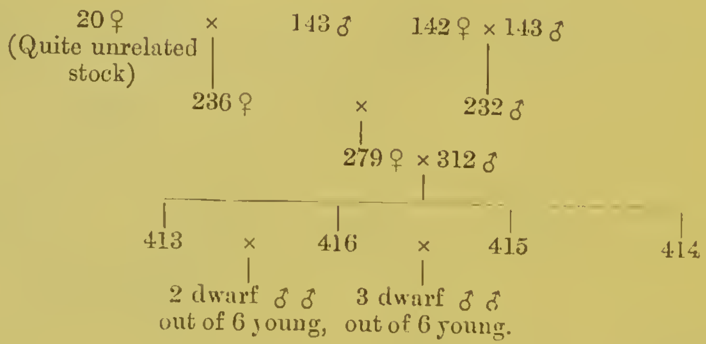
(369 ♂ is descended from 285 × 287 (see (i)).



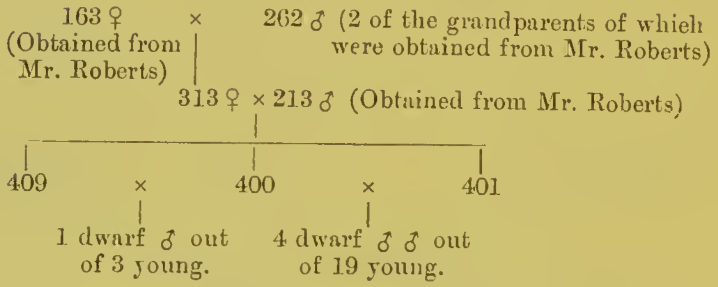
350 ♀, mentioned under (i), also contains some of the blood of Mr. Roberts' chocolates 140, 142, 143. Thus :—


142 × 143
66 ♀ (Walton and Waller's stock)
× 14 ♂ (Obtained from Steer)
220 × 217
140 × 143
278 ♀ × 262 ♂ (2 of the grandparents of which came from Mr. Roberts)
185 ♂ (Quite unrelated stock)
×
215 ♀
291 ♀
×
323 ♂
350 ♀

(i, *b.*)


20 ♀ (Quite unrelated stock)
×
143 ♂
142 ♀ × 143 ♂
236 ♀
×
232 ♂
279 ♀ × 312 ♂
413
×
416
×
415
414
2 dwarf ♂ ♂ out of 6 young,
3 dwarf ♂ ♂ out of 6 young.

(ii)


163 ♀ (Obtained from Mr. Roberts)
×
262 ♂ (2 of the grandparents of which were obtained from Mr. Roberts)
313 ♀ × 213 ♂ (Obtained from Mr. Roberts)
409
×
400
×
401
1 dwarf ♂ out of 3 young.
4 dwarf ♂ ♂ out of 19 young.

It is clear that the faculty of producing some dwarfs among the offspring is transmissible, and, though the evidence is incomplete, it seems not unlikely that all these dwarf-bearing animals have inherited the dwarf-bearing character from Mr. Roberts' stock. The probability is increased by the fact that all of Mr. Roberts' stock concerned were chocolates or albinos carrying chocolate; and as Mr. Roberts was the first to produce the chocolate breed, his chocolates are presumably closely related to each other.

Characters of the Dwarfs.

Out of a total of 16 dwarfs, one only was a female, so that it appears that there may be a partial association of sex with the dwarf character.

Of these 16 dwarfs only one has lived to maturity, and is now six months old: it is a male. Of the remainder, one male lived to the age of 11 weeks, another four weeks, a third three weeks, a fourth 15 days, a fifth six days, and the remainder were either born dead or did not live beyond the age of two days. The female was born dead.

In all the dwarfs the characters which at once attract notice are the shortness of the thick-set body, the shortness of the limbs and the unusual form of the head. The smaller size becomes more and more noticeable as the animal ages: in a new-born young the difference appears to be chiefly one of proportions.

The single dwarf now living, which was born September 20, 1908, weighed on March 15, 1909, ¾ lb.—the weight being measured by a spring balance weighing to 2 lbs. On March 29, 1909, the weight had not altered. A normal male born September 29, 1908, weighed, in the same balance, on March 29, 1909, 1½ lbs. So that, at the age of six months, this dwarf weighs just half as much as a normal male of its own age.

An examination of the skeleton shows that all the bones of the trunk and limbs are shorter and stouter than those of a normal guinea-pig, and, in the skull, the basi-cranial axis and the face are very much shortened. The shortening of the basi-cranial axis considerably alters the general form of the skull, and results in a change of position of the foramen magnum which comes to lie in the floor of the skull. Figs. 11 to 15 give a rough idea of the amount of this change. In these figures normal adult (13), new-born (14), and fœtal (15) skulls and young dwarf skulls (11 and 12) are arranged resting on the dorsal surface of the face with a pin lying across the foramen magnum; and it is seen that the skulls form a series in which the angle formed by the pin lying across the foramen magnum, with the plane of the dorsal surface of the face, continually increases, the angle being smallest in the adult normal, larger in the new-born and fœtal normal, and largest in the dwarf skulls. But this is really a misleading series, for in all the normal skulls, whatever their age, the angle made by the pin across the foramen magnum with the ventral surface of the basis cranii is fairly constant. The change of the angle made by the pin with the base line in the photograph is really a measure of the progressive development of the face in the normal skulls, and in the abnormal skulls the more marked change is due to the larger size of the angle made with the basis cranii by the line joining the mid-dorsal and mid-ventral points of the margin of the foramen magnum. Rough measurements of this angle follow:—

The median line of the ventral surface of the basis cranii is not a straight line; but the median ventral line of the presphenoid, if produced backwards, is continuous with the median ventral line of that part of the basi-occipital which forms the lips of the foramen magnum, and it is this line which I have used in making the above rough measurements.

Normal skulls.	Size of angle.
	°
Adult, old ♂ L = 6·05 cm. (see table on p. 77)	110
,, ,, ♀ ,,	119
,, ,, ♀ ,,	109
,, young, age and sex unknown, L = 5·72 cm.	115
Young, age and sex unknown, L = 4·82 cm.	124
,, ,, ,, L = 4·9 cm.	123
,, 5½ weeks ♀	125
New-born, young	120
Fœtus	119

The mean of these angles is 118°.

Skulls of dwarfs.	Size of angle.
	°
New-born, young ♂	138
,, ,, ♂	146
Young, 2 days old ♂	142
,, 6 weeks old ♂	146
,, 11 ,, ♂	146
,, 15 days old ♂	146
,, 4 weeks old ♂	146

The mean of these angles is 144°. Thus there is a difference in the mean angle of 26°.

The following table shows the values in normal and dwarf skulls of: (1) the length of the skull, measured with calipers, from the middle point of the ventral lip of the foramen magnum to the ventral tip of that narrow bit of premaxilla which runs down between the incisor teeth: this length is L (see fig. 2); (2) the greatest breadth between

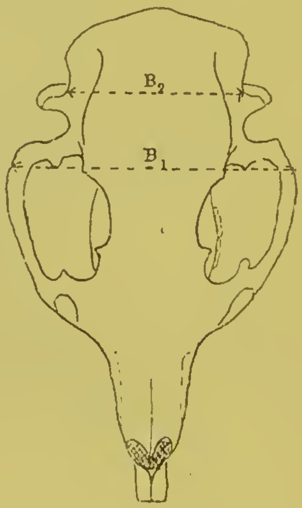


FIG. 2.

the zygomatic arches—B_1; (3) the breadth between the upper lips of the external auditory meatus of each side—B_2.

Skulls.	L.	B_1.	B_2.
	cm.	cm.	cm.
I. Normal—			
Old ♂	6·05	3·9	2·45
Old ♀	6·05	4·0	2·455
Old ♀	6·05	3·9	2·39
5 weeks	4·28	2·81	2·04
New-born	2·8	1·79	1·6
II. Dwarf—			
11 weeks old	3·38	3·05	2·02
4 weeks	3·25	2·77	1·9
15 days	2·85	2·55	1·78
6 days	2·89	2·4	1·75
2 days	2·65	broken	1·64
New-born	2·6	broken	1·64
New-born	2·76	2·12	1·66

From this we see the rate of growth is much lower in the dwarf than in the normal skull. Thus, if we subtract the values of L, B_1, B_2 of a new-born dwarf skull from the same values in the 11 weeks' dwarf skull, we obtain a rough measure of 11 weeks' growth in these values of the dwarf. And similarly from the table of normal values we can obtain the increase in L, B_1, B_2 in five and a-half weeks, *i.e.*, half the time. The results follow:—

	Cm. in L.	Cm. in B_1.	Cm. in B_2.
Increase in 11 weeks, dwarf	0·62	0·93	0·36
,, 5 ,, normal	1·48	1·02	0·44

So that the rate of increase in B_1, B_2 is less than half the normal increase in the dwarf, and the rate of increase in L is less than a quarter of the normal.

It is also interesting to notice that in the normal skull the breadth between the zygomatic arches increases with age more rapidly than the length of the skull, while the length of the skull increases with age more rapidly than the breadth of the skull between the external auditory meatus, and to compare these facts as far as possible with the corresponding facts for the dwarf skull. The comparison is shown in the following table:—

Age of skull.	$\frac{L}{B_1}$ normal.	$\frac{L}{B_2}$ normal.	$\frac{L}{B_1}$ dwarf.	$\frac{L}{B_2}$ dwarf.
Old	1·285	2·49	—	—
11 weeks	—	—	1·1085	1·67
5½ "	1·523	2·098	—	—
4 "	—	—	1·174	1·71
New-born	1·564	1·75	1·3	1·66

The modification in the form of the scapula, which is shown in figs. 4 to 7, occurs in all the dwarfs.

It may be suggested that this sport is the result of some variation in the conditions of development—some irregularity of gestation. But it seems more probable that it is due to a variation in the germ plasm, and if further evidence should confirm the suggestion that there is a partial association of male sex with the dwarf condition, then there can be no doubt that the variation is germinal.*

It still remains to be seen whether the dwarfs are capable of producing young. If they should do so, they would found a race differing from the type at least as much as most mammalian species differ from one another.

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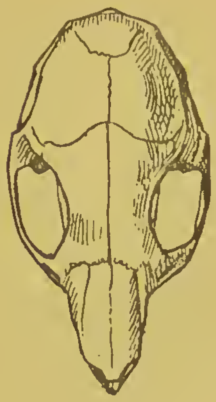
* *Additional Note, November* 2, 1909.—The number of dwarfs up to the present date is 25. Their incidence among the several families is remarkable, and shows very curious sex-ratios, but the evidence is not yet sufficiently complete to make analysis possible. The distribution is as follows:—

Parents.		Normal offspring.		Dwarf offspring.	
♀.	♂.	♀.	♂.	♀.	♂.
286	287	2	3	—	1
400	401	7	17	—	7
409	401	2	1	—	1
413	416	—	3	—	3
415	416	1	8	—	4
571	401	2	3	—	1
571	312	2	5	—	1
572	369	1	—	—	1
572	416	5	6	3	1
586	416	—	2	1	—
586	550	3	1	1	—
Totals		25 ♀	49 ♂	$\underbrace{\text{5 ♀ \qquad 20 ♂}}_{\text{25 dwarfs.}}$	

3



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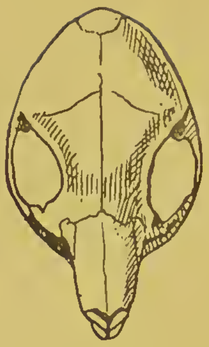

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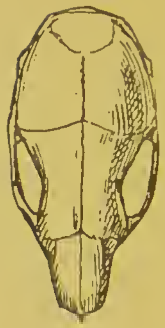

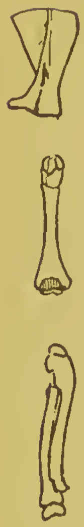

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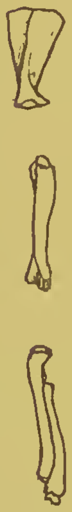

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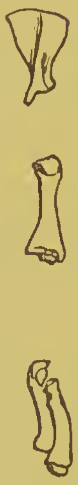

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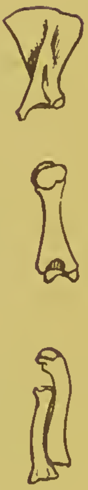

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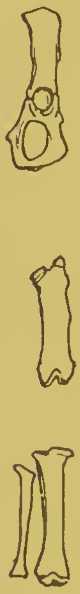

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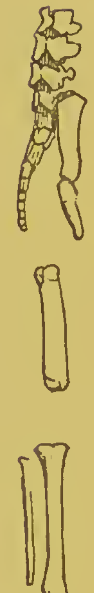

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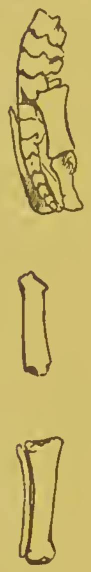

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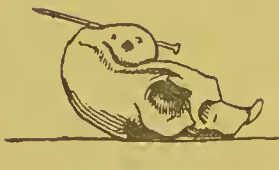

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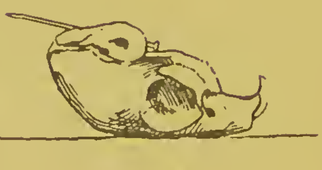

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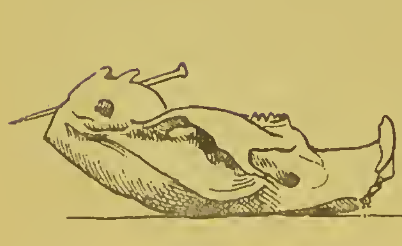

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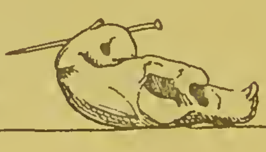

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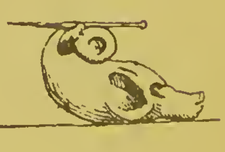

15

My thanks are due to Prof. Bateson for his kindness in helping me in the interpretation of the results which are stated here, and for criticising this paper.

The expenses of the experiments were partly defrayed by grants from the Royal Society and from the Cambridge Botanic Garden Experiments Fund.

DESCRIPTION OF PLATE.

(All the figures are tracings from a photograph.)

1.—Skull of a "dwarf" 6 days old.

2 and 3.—Normal skulls: 2 of about the same length, 3 of about the same breadth, to show the difference in proportions.

4 and 5.—Scapula and arm bones of a normal new-born guinea-pig.

6 and 7.—Scapula and arm bones of dwarfs, respectively new-born and aged 6 days.

8.—Pelvic girdle, femur, tibia, and fibula of dwarf, aged 6 days.

9 and 10.—Posterior end of vertebral column, with attached pelvis of normal new-born and dwarf new-born guinea-pigs respectively.

11 to 15.—Skulls of guinea-pigs resting on the dorsal surface of the face, with a pin lying across the foramen magnum, to show the angle made by this pin (see p. 75) with the surface on which the skull is resting. 11, dwarf new-born; 12, dwarf, 6 days old; 13, adult, normal; 14, new-born, normal; 15, fœtal normal.

CORRIGENDA IN REPORT IV.

Page 3, line 16, *for* "1 purple red" *read* "1 purple round."

Page 10, line 18, *for* "3707" *read* "3757."

Page 10, line 19, *for* "939" *read* "935."

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